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# The Great Basin Naturalist

VOLUME 39, 1979

EDITOR: STEPHEN L. WOOD

THE GREAT BASIN NATURALIST
BYU PROVO, UTAH
1939

PUBLISHED AT BRIGHAM YOUNG UNIVERSITY, BY
BRIGHAM YOUNG UNIVERSITY

## TABLE OF CONTENTS

### Volume 39

### Number 1 - March 31, 1979

Phlox longifolia Nutt. (Polemoniaceae) complex of North America. Frederick J. Peabody ........ 1

Diatom floristics and succession in a peat bog near Lily Lake, Summit County, Utah. Shobha A. Jatkar, Samuel R. Rushforth, and Jack D. Brotherson ........ 15

Vegetational response to three environmental gradients in the salt playa near Goshen, Utah County, Utah. Michael G. Skougard and Jack D. Brotherson ........ 44

Distribution of sculpins in the Clearwater basin, Idaho. O. Eugene Maughan and Gary E. Saul ........ 59

Phytoseiid predators of mite pests in Utah apple orchards. Clive D. Jorgensen and Vichitra Mongkolprasith ........ 63

Subspecies specificity of gall forms on *Chrysothamnus nauseosus*. E. Durant McArthur, Charles F. Tiernan, and Bruce L. Welsh ........ 81

Homing by a pygmy rabbit. Jeffrey S. Green and Jerran T. Flinders ........ 88

Beetles from the environs of Lake Powell in southern Utah and northern Arizona. Dorald M. Allred and Vasco M. Tanner ........ 89

Ants from northern Arizona and southern Utah. Dorald M. Allred and Arthur C. Cole ........ 97

### Number 2 - June 30, 1979

Review of tularemia in Utah and the Great Basin, Harold E. Stark ........ 103

Chemical composition of some important plants of southeastern Utah summer ranges related to mule deer reproduction. Jordan C. Pederson and K. T. Harper ........ 122

Emergence data and artificial rearing media for an aspen bark beetle, *Trypophloeus populi* (Coleoptera: Scolytidae). David A. Stewart, Gary M. Booth, Jerold L. Petty 129

New synonymy and new species of American bark beetles (Coleoptera: Scolytidae), Part VIII. Stephen L. Wood ........ 133

Annual energy budgets for three common rodent species in the northern Great Basin. R. Kent Schreiber ........ 143

Preliminary survey of raptor species in the Manti Division, Manti-LaSal National Forest. Stephen G. Jones ........ 155

Vegetation response to a moisture gradient on an ephemeral stream in central Arizona. Deborah Ann Bloss and Jack D. Brotherson ........ 161

Ecological and community relationships of *Eriogonum corymbosum* (Polygonaceae) in the Uinta Basin, Utah. Jack D. Brotherson and Karen J. Brotherson ........ 177

Variation in hemoglobin types in the deer mouse (*Peromyscus maniculatus*( along an altitudinal gradient. David Wasserman and Donald J. Nash ........ 192

First record of *Patapius spinosus* in Idaho and Nevada (Hemiptera: Leptopodidae). Donald R. Brothers ........ 195

Bee visitation of *Phlox bryoides* (Polemoniaceae). V. J. Tepedino ........ 197

Ecological distribution of rodents in Canyonlands National Park, Utah. David M. Armstrong ........ 199

## Number 3 - September 30, 1979

getative and edaphic factors affecting abundance and distribution of small mammals in southeast Oregon. George A. Feldhamer ........ 207
fluence of precipitation and temperature on ring, annual branch increment, and needle growth of White Fir and Douglas-fir in central Utah. John D. Shane and Kimball T. Harper ........ 219
udies in Nearctic desert sand dune Orthoptera, Part XVI: A new black *Stenopelmatus* from the Mescalero sands. Ernest R. Tinkham ........ 226
tential use of Great Salt Lake water for lobster culture. Roger W. Mickelsen, Richard A. Heckmann, and Rex C. Infanger ........ 231
earctic stonefly genera as indicators of ecological parameters (Plecoptera: Insecta). Richard W. Baumann ........ 241
mpetitive displacement as a factor influencing phytoplankton distribution in Utah Lake, Utah. Lorin E. Squires, Mark C. Whiting, Jack D. Brotherson, and Samuel R. Rushforth ........ 245
round nesting and aggressive behavior by the Swainson's Hawk (*Buteo swainsoni*). Neil D. Woffinden and James A. Mosher ........ 253
esponse of reptile populations to different land management practices on the Idaho National Engineering Laboratory Site. Timothy D. Reynolds ........ 255
ecreases of juniper woodland in the Utah and Salt Lake valleys since settlement. E. M. Christensen and J. D. Brotherson ........ 263
mpetition between harvester ants and rodents in the cold desert. Dan S. Landeen, Clive D. Jorgensen, and H. Duane Smith ........ 267
od habits of burrowing owls in southeastern Idaho. R. L. Gleason and T. H. Craig ........ 274
ora of the Lee Creek valley, Alberta. R. Keith Shaw ........ 277
imates of fescue grasslands of mountains in the western United States. T. Weaver ........ 284
onefly (Plecoptera) records from the basin ranges of Nevada and Utah. Andrew L. Sheldon ........ 289

## Number 4 - December 31, 1979

raginaceae of the southwestern United States. Larry C. Higgins ........ 293
nomiopsyllinae (Siphonaptera: Hystrichopsyllidae), II. The genera *Callistopsyllus*, *Conorhinopsylla*, *Megarthroglossus*, and *Stenistomera*. Vernon J. Tipton, Harold E. Stark, and John A. Wildie ........ 351
aryotypes of four *Artemisia* species: *A. carruthii*, *A. filifolia*, *A. frigida*, and *A. spinescens*. E. Durant McArthur and C. Lorenzo Pope ........ 419
ariation in leaf anatomy and $Co_2$ assimilation in *Sitanion hystrix* ecotypes. Warren P. Clary ........ 427
dex to Volume 39 ........ 433

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Volume 39 No. 1
March 31, 1979
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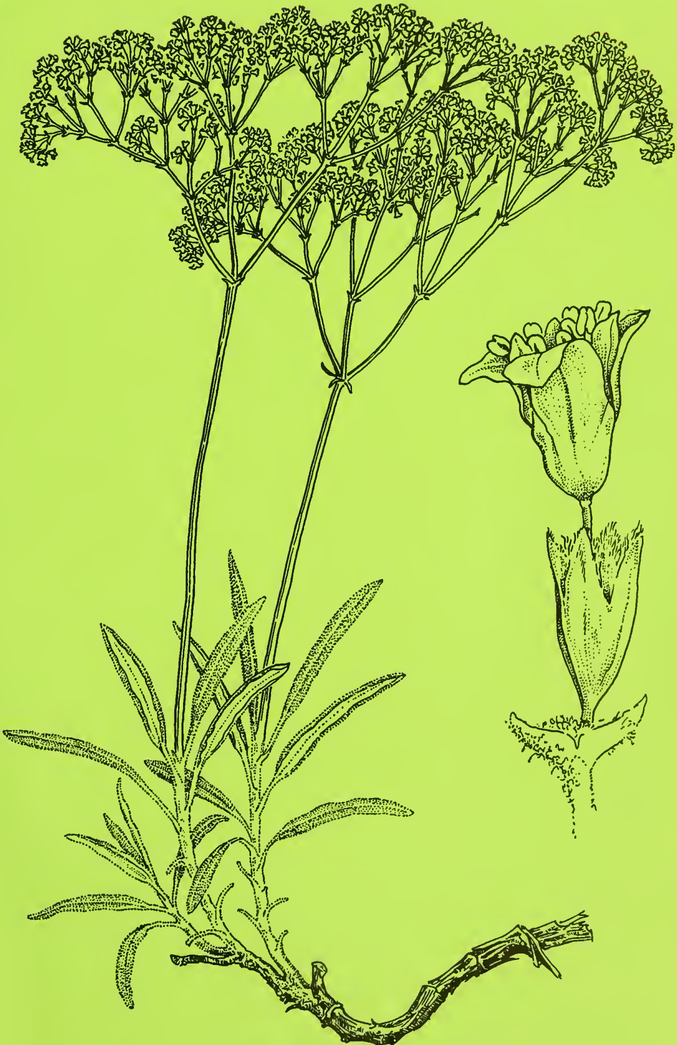

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11-78 650 34941

The Great Basin Naturalist

Published at Provo, Utah, by
Brigham Young University

ISSN 0017-3614

Volume 39 March 31, 1979 No. 1

# PHLOX LONGIFOLIA NUTT. (POLEMONIACEAE) COMPLEX OF NORTH AMERICA[1]

Frederick J. Peabody[2]

Abstract.— Over 1,000 herbarium specimens including 24 type specimens were examined in an attempt to achieve a clearer understanding of the *Phlox longifolia* complex. Four variables were measured for each specimen and the data were statistically analyzed by discriminant analysis. Using a previously published system of classification for the complex, approximately 73 percent of the measured variation among the specimens was accounted for by that system. The clustering patterns produced in this first analysis indicated that a more conservative approach would be advisable. The formulation and subsequent application of a modified system produced a grouping of specimens that accounted for 95 percent of the measured variation for the four morphological characters considered. From four species and seven subspecies previously recognized, one species with five varieties is proposed. The typification of *Phlox longifolia* Nutt. and other related taxa is resolved.

The classification of plants belonging to the *Phlox longifolia* Nutt. complex has been fraught with difficulties from the very beginning of the nomenclatural history of the group. Infraspecific taxa have been attributed to one species and then another, new species have been proposed to deal with the great range of diversity within the group, and confusion has arisen as to the level or rank of recognition best suited for any one entity. The present study has two basic objectives: first, to correlate recent collections and current descriptions with the type material; and second, to review the classification of the complex in light of a broad sample.

The method proposed for the solution of the problem is twofold: A test of the most recently proposed classification system (Wherry 1955), and then a similar test of a modified system proposed by me. Statistical analyses were conducted with the use of the IBM 360 computer using the SPSS V602 program for discriminant analysis from the Statistical Package for the Social Sciences available at Brigham Young University Computer Center. Over 1,000 specimens from nine western United States herbaria were examined and included in the sample. Twenty-four type specimens from an additional 13 herbaria were also examined. Classical methods of taxonomic research were employed in reviewing type material and adjusting the nomenclature in order to bring the treatment of this complex into agreement with the International Code of Botanical Nomenclature (Stafleu et al. 1972).

The variables tested were the following: vestiture of the inflorescence herbage, corolla tube length, leaf length, and leaf width. Over the past 160 years of taxonomic history these four morphological features have proved to be adequate for separation into infraspecific taxa. They are also easily measured from dried and mounted herbarium specimens.

Following the descriptions of each taxon in the taxonomy section is a citation of representative material examined, followed by a number indicating the total number of specimens examined and placed within that taxon. The standard abbreviations of herbaria are those of Holmgren and Keuken (1974). Type specimens were examined and photographed and the photographs deposited in the Herbarium of Brigham Young University (BRY); they are indicated by an asterisk (*) following the herbarium symbol designation in the list of synonyms. The standard abbreviations of serial publications are those of the Torrey Botanical Club (1969). The standard abbreviations of separate works are those of Lawrence (1968). Statistical information is available from the author upon request.

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## ACKNOWLEDGMENTS

The author wishes to acknowledge the many herbaria and their staffs for the loan of material for examination. Appreciation is also extended to Dr. Stanley L. Welsh for valuable assistance in research and preparation. The constant support of Robyne, my wife, is deeply appreciated.

## NOMENCLATURAL HISTORY

Thomas Nuttall (1834) described *Phlox longifolia* from material gathered by Wyeth in 1833 from the "valleys of the Rocky Mountains generally". Heller (1897) elevated Torrey's (1859) *P. speciosa* var. ? *stansburyi* to species rank in a cryptic note which affords little information as to its salient features. Subsequent workers influencing this complex include: E. Nelson (1899), Brand (1907), Jones (1895, 1908), A. Nelson (1909, 1912, 1924, 1931), Wherry (1938, 1939, 1940, 1941, 1942, 1943, 1944, 1955, 1956), Peck (1941), Jepson (1943), and Mason (1951). Over the past 163 years, 16 species and 36 infraspecific taxa have been named within this complex. Of the 52 names proposed in this group only 5 are recognized as valid in the present study.

## TAXONOMY OF PHLOX LONGIFOLIA COMPLEX

Taprooted perennials, 0.3–5 dm tall, from a lignous base; leaves cauline, opposite, sometimes alternate above, 5–70 (100) mm long, 1–7 mm wide, linear to oblanceolate; upper cauline leaves glabrous, pubescent or glandular-pubescent; lower cauline leaves glabrescent, basally connate or distinct; pedicels (5) 10–40 (50) mm long, glabrous, pubescent, or glandular-pubescent; calyx of 5 aristate to cuspidate, basally connate sepals with prominent herbaceous midribs, glabrous except on adaxial surface, pubescent or glandular-pubescent, distinct chartaceous intercostal membranes either plicate or flat; corolla tube (8) 10–28 mm long, usually glabrous but sometimes sparsely pilose without, the limb 5–15 mm long, incisorate, erose, or entire; stamens unequally inserted on the corolla tube, included or scarsely excerted; style 3-cleft, the ovary 3-loculed, the seeds 1 (2–4) per locule.

## KEY TO VARIETIES

1. Inflorescence herbage glabrous except calyx within, or pubescent on upper leaf margins, pedicels and calyx without; leaves linear .................................................................................................................... *P. longifolia* var. *longifolia*

Inflorescence herbage glandular-pubescent, rarely simply pubescent (var. *longipes* and var. *viridis*); leaves linear to oblanceolate .......................................... 2

2(1). Corolla tube 22–28 mm long; southwestern New Mexico westward across Arizona to southern and western Utah, Nevada and eastern California ........................................................................................... *P. longifolia* var. *stansburyi*

Corolla tube 12–19 mm long; variously distributed throughout western North America .......................................................................................... 3

3(2). Leaves (even upper) distinctly oblanceolate, 3–5 mm wide; inflorescence herbage glandular-pubescent; internodes well spaced; stems stout and often trailing; southwestern South Dakota westward to eastern California ..... *P. longifolia* var. *brevifolia*

Leaves linear to linear-lanceolate, 1–3 mm wide; inflorescence herbage rarely nonglandular-pubescent; internodes well spaced or congested; stems slender and usually ascending; variously distributed throughout western North America .......... 4

4(3). Leaves 45–70 mm long, 2.5–4 mm wide; internodes well spaced; northern New Mexico and Arizona through Nevada, Utah, and western Colorado, narrowly extending into southern Idaho and Oregon .......... *P. longifolia* var. *longipes*

Leaves 16–35 mm long, 1–2 mm wide; internodes usually congested; Washington, Oregon, Idaho, extending narrowly into extreme northern Utah and Nevada .......... *P. longifolia* var. *viridis*

## *Phlox longifolia* Nutt. var. *longifolia*

*Phlox longifolia* Nutt., J. Acad. Nat. Sci. Philadelphia 7: 41. 1834. Holotype: Valleys of the Rocky Mts. generally, 1833, *Wyeth s.n.* (BM°). Isotype (K°).

*P. humilis* Dougl. ex Hook., Fl. Boreali-Amer. 2: 72. 1838. Holotype: Oregon; barren sandy plains of the Columbia, 1826, *Douglas s.n.* (K°).

*P. speciosa* Pursh var. *B* Dougl. ex Hook., Fl. Boreali-Amer. 2: 72. 1838. Holotype: Oregon; on the summit of the Blue Mountains and subalpine range of the Rockies near perpetual snow, no date, *Douglas s.n.* (K°).

*P. sabini* Hook. *pro syn.*, Fl. Boreali-Amer. 2: 72. 1838.

*P. speciosa* Pursh var. *linearifolia* Hook., Hooker's J. Bot. Kew Gard. Misc. 3: 289. 1851. Holotype: Valley of the Kooskooskie River and adjoining plains, no date, *Douglas s.n.* (K°).

*P. linearifolia* (Hook.) A. Gray, Proc. Amer. Acad. Arts 8: 255. 1870.

*P. longifolia* Nutt. f. *humilis* (Dougl. ex Hook.) Voss, Vilmorin Blumengartn 1: 681. 1894.

*P. longifolia* Nutt. ssp. *marginata* Brand, Das Pflanzenreich $4^{250}$: 65. 1907. Holotype: Oregon; steep grassy slopes near Snake River, where it is common, 23 May 1901, *Cusick 2517*, (G°).

*P. longifolia* Nutt. ssp. *marginata* Brand var. *humilis* (Dougl. ex Hook.) Brand, Das Pflanzenreich $4^{250}$: 66. 1907.

*P. longifolia* Nutt. ssp. *linearifolia* (Hook.) Brand, Das Pflanzenreich $4^{250}$: 66. 1907.

*P. patula* A. Nelson, Univ. Wyoming Publ. Sci., Bot. 93: 47. 1924. Holotype: Colorado; Platte Canyon, 19 May 1894, *A. Nelson 1589*, (RM°).

*P. marginata* (Brand) A. Nelson, Amer. J. Bot. 18: 434. 1931.

*P. cortezana* A. Nelson, Amer. J. Bot. 18: 434. 1931. Holotype: Colorado; Montezuma Co., roadside between Cortez and Mesa Verde National Park, 11 May 1925, *A. Nelson 10436* (RM°).

*P. longifolia* Nutt. ssp. *humilis* (Dougl. ex Hook.) Wherry, Proc. Acad. Nat. Sci. Philadelphia 90: 135. 1938.

*P. longifolia* Nutt. ssp. *calva* Wherry, Proc. Acad. Nat. Sci. Philadelphia 90: 136. 1938. Holotype: Idaho; Butte Co., 13 miles by road southwest of Darlington (43°41½'; 113°34½'), 21 June 1931. *E. T. Wherry s.n.* (PH°).

*P. longifolia* Nutt. ssp. *typica* Wherry, *pro. typ.* Notul. Nat. Acad. Nat. Sci. Philadelphia 87: 5. 1941.

*P. longifolia* Nutt. ssp. *cortezana* (A. Nelson) Wherry, Notul. Nat. Acad. Nat. Sci. Philadelphia 87: 5. 1941.

*P. grahamii* Wherry, Brittonia 5: 60. 1943. Holotype: Utah; Uinta Co., talus slopes west side of Green River, south of mouth of Sand Wash, 4500 ft., elevation, 27 May 1923, *Graham 7884* (CM°).

*P. longifolia* Nutt. ssp. *a-longifolia* Wherry, *pro. typ.* Morris Arb. Bull. 3: 90. 1956.

Plants short to tall, 0.5–5.0 dm; internodes more or less congested or well spaced; leaves opposite, upper leaves glabrous or pubescent, nonglandular, (10) 20–50 (60) mm long, 1.0–2.5 mm wide, linear to linear-lanceolate; calyx glabrous or pubescent with intercostal membranes either plicate or flat; corolla tube 12–16 mm long (Fig. 1).

**Representative material.**— *Huntley 889 (WTU); Parker 578 (OSC); Davis 334 (IDS); Vickery 550 (ARIZ); Cronquist 6237 (COLO); Thompson 11316 (MONTU); Brown 3780 (UNM).* 645.

**Distribution.**— Central and eastern Washington, eastern and central Oregon, southern Idaho, southwestern Montana, southwestern Wyoming, Nevada, Utah, western Colorado,

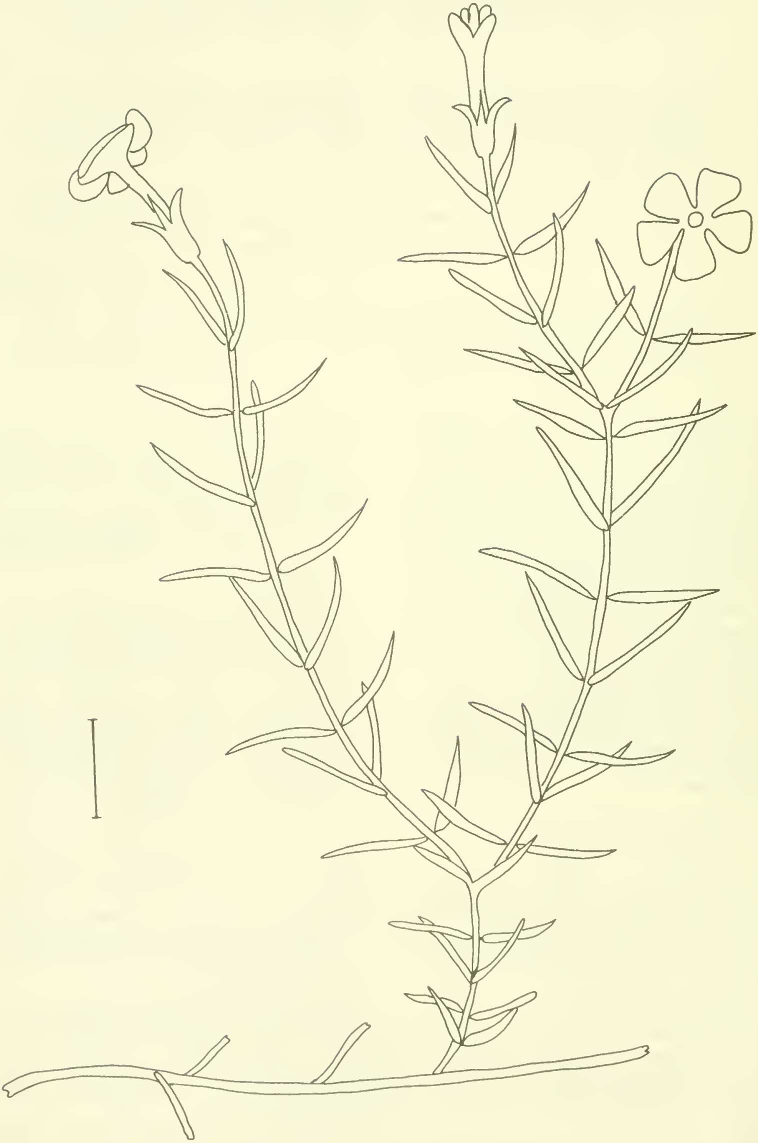

Fig. 1. *Phlox longifolia* Nuttal var. *longifolia*. ISOTYPE: Valleys of the Rocky Mts. generally. Wyeth s.n., no date (BMI°). Measure bar equals 1 cm.

extreme northwestern New Mexico, northern Arizona, and extreme southeastern California. This nonglandular form is the most abundant variety in northern and mesic localities (Fig. 2).

**Notes**— Nuttall (1834) described *Phlox longifolia* based on a specimen with long leaves as compared to the caespitose representatives of the genus, sic. *P. caespitosa*, *P. hoodii* etc. Douglas (1838) described *P. humilis* based on material similar to that of Nuttall's *P. longifolia*, selecting this epithet because the leaves were smaller than those of *P. speciosa* already described by Pursh (1814) and Lindley (1830). Gray (1870) rectified the situation by placing Douglas's *P. humilis* in synonymy with Nuttall's *P. longifolia*. At the same time Gray proposed a new species which had longer leaves and distinct replication of the intercostal membranes of the calyx, naming this species *P. linearifolia* (Hook.) A. Gray.

With the passage of years since the work of Gray (1870) and the activity of post-Grayan monographers, the taxonomy of this group became extremely obscured. Nuttall's type was disregarded, Gray's *Phlox linearifolia* fell out of use and bi- or trinomials were applied to erroneous taxa. The longer-leaved and taller *P. linearifolia* became commonly known as *P. longifolia*, leaving the type of *P. longifolia* to be erroneously renamed at various infraspecific levels. Among these renamings are: *P. longifolia* ssp. *marginata* var. *humilis* (Dougl. ex Hook.) Brand (1907), *P. longifolia* ssp. *humilis* (Dougl. ex. Hook.) Wherry (1938), and *P. longifolia* f. *humilis* (Dougl. ex Hook.) Voss (1894). This unfortunate condi-

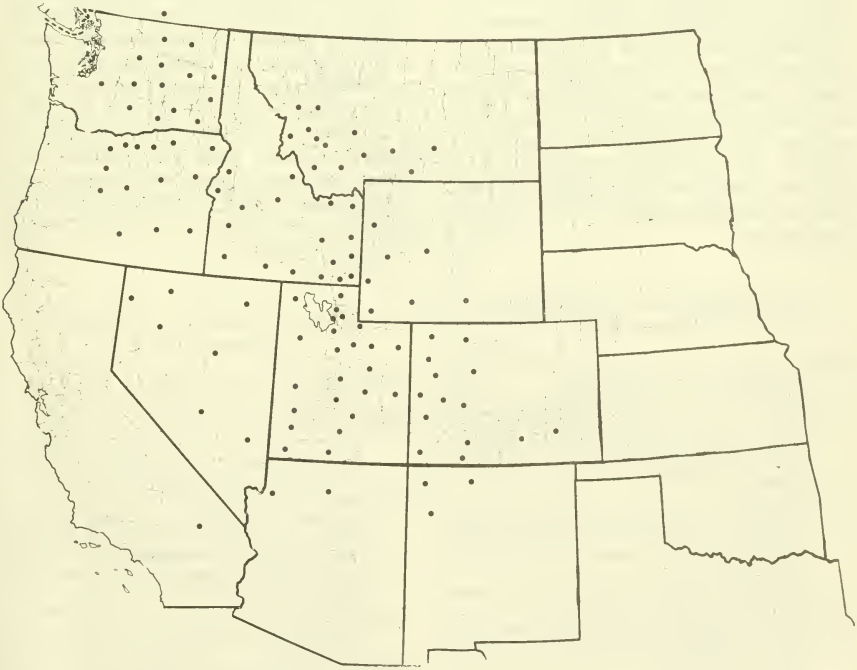

Fig. 2. Distribution of *Phlox longifolia* Nutt. var. *longifolia* over western North America.

tion has continued to the present day, causing taxonomic confusion within the complex.

Wherry (1943) proposed *Phlox grahamii* Wherry as an intermediate form between two genera (*Phlox* and *Microsteris*). His reasons were that the plant in question (Graham 7884) combines morphological characters of each genus. It is perennial and rather tall with well-spaced internodes and a distinct corolla tube like *Phlox.* The leaves, however, are relatively small, few, and some are lobed near the base; the corolla tube is strongly flaring at the base and the inflorescence is sparse as in the genus *Microsteris.*

Upon examination of this specimen, which unfortunately is the only specimen of this species ever collected or reported, I have found that it is copiously infested with a rust (*Puccinia plumbaria* Peck) according to identification made with Arthur (1962). The base of the corolla tube is filled with hyphae, causing it to flare, and one of the few upper leaves bears a number of aecia imbedded in its epidermis that caused it to lobe abnormally as it elongated in growth. The general health of the plant was obviously very poor and all of the features noted by Wherry as resembling the genus *Microsteris* are, in my opinion, the result of teratology. *Phlox grahamii* appears to be a diseased *P. longifolia* var. *longifolia* and is therefore reduced to synonymy.

### *Phlox longifolia* Nutt. var. *stansburyi* (Torr.) A. Gray

*Phlox longifolia* Nutt. var. *stansburyi* (Torr.) A. Gray, Proc. Am. Acad. Arts 8:255. 1870.

*P. speciosa* Pursh var. ? *stansburyi* Torr., Rep. U.S. Mex. Bound. Surv. 2: 145. 1859. Holotype: New Mexico; Dona Ana Co., gravelly hills near the Organ Mountains, 30 April 1852, *Bigelow s.n.* (NY).

*P. stansburyi* (Torr.) Heller, Bull. Torrey Bot. Club 24: 478. 1897.

*P. longituba* Heller, Muhlenbergia 2: 228. 1906. Isotype (?): California; Inyo Co., Sierra foothills west of Bishop in coarse granite sand, 23 May 1906, *Heller 8320* (BM°).

*P. stansburyi* (Torr.) Heller ssp. *eu-stansburyi* Brand, Das Pflanzenreich $4^{250}$: 66. 1907.

*P. superba* Brand, Das Pflanzenreich $4^{250}$: 67. 1907. Holotype: Nevada; Nye Co., Tonopah, May 1905, *Brown s.n.* (UC°).

*P. stansburyi* (Torr.) Heller ssp. *eu-stansburyi* Brand f. *longituba* (Heller) Wherry, Notul. Nat. Acad. Nat. Sci. Philadelphia 113: 4. 1942.

*P. stansburyi* (Torr.) Heller ssp. *superba* (Brand) Wherry, Notul. Nat. Acad. Sci. Philadelphia 113: 4. 1942.

Plants moderately tall, 1.5–4.0 dm, internodes well-spaced, 3–6 cm long; leaves opposite, upper leaves somewhat glandular-pubescent, 22–39 mm long, 2.1–3.8 mm wide, linear to linear-lanceolate; calyx glandular-pubescent with the intercostal membranes usually flat; corolla tube 22–28 mm long (Fig. 3).

**Representative material**— *Arnott 37, (WTU), Maguire 25123 (OSC), Ferris 8054 (MONTU), Hershey 2826 (UNM), Wooton s.n. (COLO), Wooton s.n. (ARIZ).* 38.

**Distribution**— Western New Mexico, Arizona, western Utah, Nevada, and extreme eastern California (Fig. 4).

**Notes**— The taxon *stansburyi* proves to fit into *P. longifolia* quite well because it has many characters in common with other varieties. The long corolla tube usually cited as the distinguishing feature merely represents a point in a continuum of corolla tube length within this complex. Other features are essentially the same as in *P. longifolia* (*sensu lato*). As defined here var. *stansburyi* occurs not only in southwestern New Mexico and adjacent Arizona (Wherry 1956) but also in northern Arizona, Utah, and Nevada. As it passes northward it appears to assume some of the characteristics of other varieties, most noticeably reduction in leaf size and length of the corolla tube.

### *Phlox longifolia* Nutt. var. *brevifolia* (A. Gray) A. Gray

*Phlox longifolia* Nutt. var. *brevifolia* (A. Gray) A. Gray, Synop. Fl. N. Amer. Vol. 2 Pt. 1: 133. 1878.

*P. longifolia* Nutt. var. *stansburyi* (Torr.) A. Gray f. *brevifolia* A. Gray, Proc. Amer. Acad. Arts 8: 255. 1870. Lectotype: Nevada; Ormsby Co., near Carson City, 1865. *Anderson s.n.* (GH°).

*P. longifolia* Nutt. var. *stansburyi* (Torr.) A. Gray subvar. *brevifolia* (A. Gray) Watson, C. King, Report of the Geographical Expl. 40th Parallel 5: 261. 1871.

*P. stansburyi* (Torr.) Heller var. *brevifolia* (A. Gray) E. Nelson, Wyoming Agric. Exp. Sta. Annual Rep. 9: 27. 1899.

*P. stansburyi* (Torr.) Heller ssp. *eu-stansburyi* Brand var. *brevifolia* (A. Gray) Brand, Das Pflanzenreich $4^{250}$: 66. 1907.

*P. grayi* Wooton & Standley, pro. syn. Contr. U.S. Nat. Herb. 16: 161. 1913.

*P. longifolia* Nutt. ssp. *brevifolia* (A. Gray) H. Mason, Abrams Ill. Fl. Pac. States 3: 409. 1951.

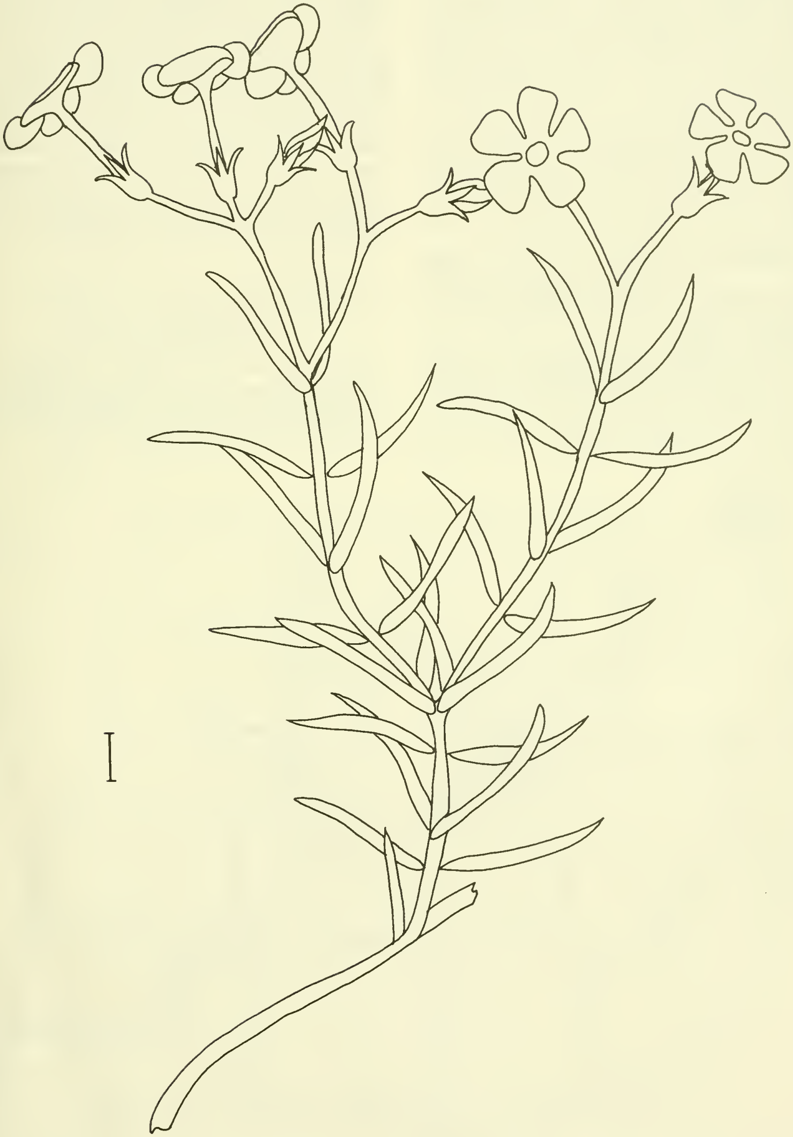

Fig. 3. *Phlox longifolia* Nutt. var. *stansburyi* (Torr.) Gray. TOPOTYPE: New Mexico, Doña Ana Co., in the Organ Mountains. E. O. Wooton s.n. 28 May 1905 (WTU°). Measure bar equals 1 cm.

Plants shorts, often trailing, 1–3 dm tall, internodes well spaced, 1–4 (5) cm long; leaves opposite, upper leaves glandular-pubescent, 16–30 mm long, 3–5 (6) mm wide, distinctly oblanceolate; upper sometimes linear-lanceolate; calyx glandular-pubescent, intercostal membranes usually flat; corolla tube 13–15 mm long (Fig. 5).

**Representative material.**– *Cronquist 8894 (WTU), Lenz 21826 (OSC), Forewood s.n. (K), Welsh 9689 (BRY), Christensen s.n. (BRY), Blauer 7 (BRY), Palmer 308 (GH), Anderson s.n. (GH)*. 67.

**Distribution.**– Extreme southwest South Dakota, central western Colorado, northern Arizona, Utah, Nevada, and extreme eastern California (Fig. 6).

**Notes.**– Variety *brevifolia* has been named under innumerable combinations over its taxonomic history. Gray's (1870, 1878) and Watson's (1871) transference of this taxon from one rank to another betrays its complexity. Of all varietal names applied over the past years, Gray's var. *brevifolia* antedates all and is chosen as the legitimate name. Because Gray indicated no type in the publication of this variety, a lectotype (Wherry 1955) has been designated (the reader is referred to the list of synonyms). It is estimated that the range of this taxon extends further eastward than any other within this complex, crossing the Continental Divide through Wyoming and into the Black Hills of southwestern South Dakota (fide Forewood 1888).

### *Phlox longifolia* Nutt. var. *longipes* (M. E. Jones) M. E. Peck

*Phlox longifolia* Nutt. var. *longipes* (M. E. Jones) M. E. Peck, Mann. Higher PLS. Oregon 571. 1941.

*P. linearifolia* (Hook.) A. Gray var. *longipes* M. E. Jones, Contr. W. Bot. 12: 53. 1908. Holotype: Idaho;

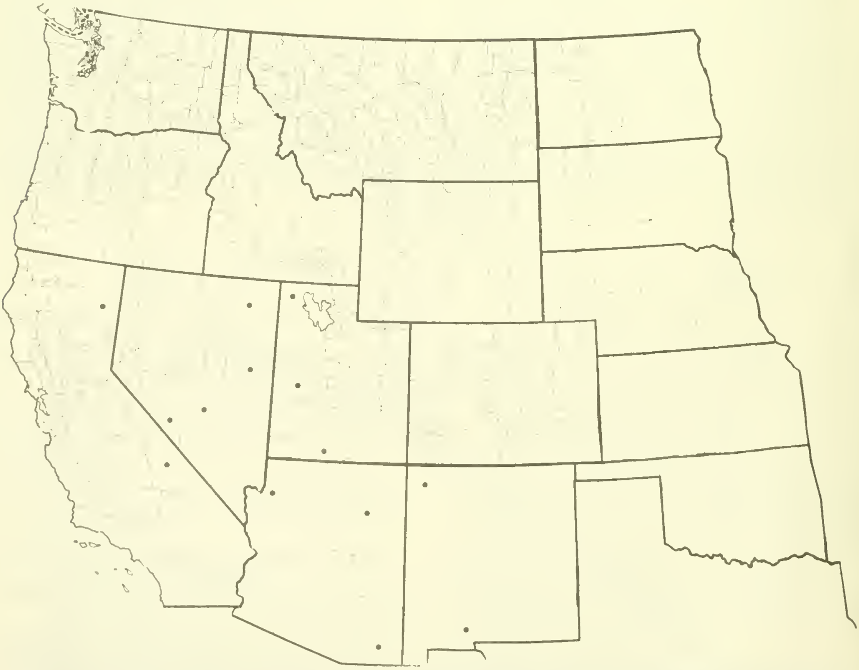

Fig. 4. Distribution of *Phlox longifolia* var. *stansburyi* (Torr.) Gray over western North America.

Washington Co., Weiser, 28 April 1900, *Jones s.n.* (POM°).

*P. longifolia* Nutt. var. *puberula* E. Nelson, Wyoming Agric. Exp. Sta. Annual Rep. 9: 26. 1899. Holotype: Wyoming; Uinta Co., Evanston, 5 June 1898, *A. Nelson* 4544 (RM°).

*P. viscida* E. Nelson, Wyoming Agric. Exp. Sta. Annual Rep. 9: 25. 1899. Holotype: Oregon; Columbia Co., Blue Mountains, 15 July 1896, *Piper 2397* (US°).

*P. stansburyi* (Torr.) Heller ssp. *compacta* Brand var. *viscida* (E. Nelson) Brand, Das Pflanzenreich $4^{250}$: 67. 1907.

*P. stansburyi* (Torr.) Heller ssp. *compacta* Brand var. *puberula* (E. Nelson) Brand, Das Pflanzenreich $4^{250}$: 67. 1907.

*P. stansburyi* (Torr.) Heller ssp. *eu-stansburyi* Brand var. *brevifolia* (A. Gray) Brand subvar. *microcalyx* Brand, Das Pflanzenreich $4^{250}$: 67. 1907. Holotype: Arizona; Yavapai Co., Prescott Mountain District, 1876, *Palmer 391* (G°).

*P. puberula* (E. Nelson) A. Nelson, Manual Bot. Rocky Mts.: 397. 1909.

*P. longifolia* Nutt. var. *filifolia* A. Nelson. Bot. Baz. (Crawfordsville) 54: 143. 1912. Holotype: Idaho; Blaine Co., Ketchum midst sagebrush, stream bottoms, alt. 5887, 19 July 1911, *A. Nelson 1192* (RM°).

*P. longifolia* Nutt. ssp. *compacta* (Brand) Wherry, Proc. Acad. Nat. Sci. Philadelphia 93: 135. 1938.

*P. longifolia* Nutt. ssp. *longipes* (M. E. Jones) Wherry, Proc. Acad. Nat. Sci. Philadelphia 93: 135. 1938.

*P. viridis* E. Nelson ssp. *longipes* (M. E. Jones) Wherry, Morris Arb. Bull. 3: 88. 1955.

*P. viridis* E. Nelson ssp. *compacta* (Brand) Wherry, Baileya 4: 98. 1956.

Plants moderately tall 1.5–4.0 dm, internodes somewhat congested or well-spaced 1–5 cm long; leaves opposite, upper leaves glandular-pubescent, 3–10 (15) mm long, 1.7–3.6 mm wide, linear to linear-lanceolate; calyx glandular-pubescent with the intercostal membranes usually flat; corolla tube 14–18 mm long (Fig. 7).

**Representative material.**— *Whites 1037 (WTU), Peck 7790 (OSC), Davis 3082 (IDS), Cottam 5062 (ARIZ), Clokey 7630 (MONTU), Clark s.n. (UNM), Hitchcock 20432 (COLO).* 122.

**Distribution.**— Eastern Oregon, southern Idaho, Utah, western and southern Colorado, Nevada, northern Arizona, northwestern

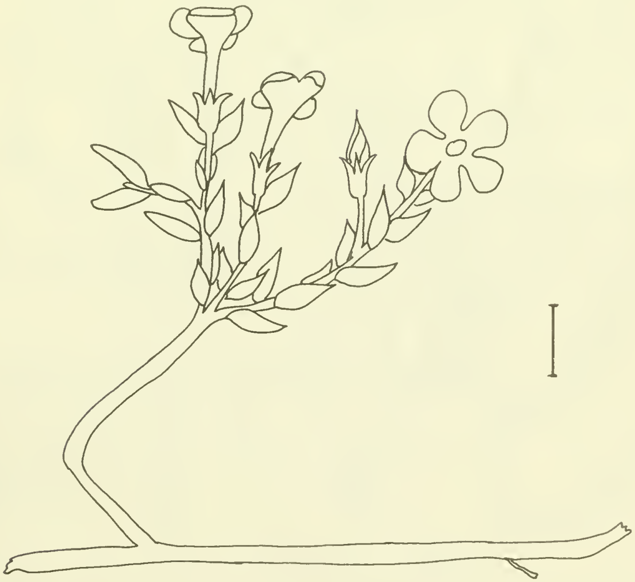

Fig. 5. *Phlox longifolia* Nutt. var. *brevifolia* Gray. COLLECTION: South Dakota, Black Hills. W. H. Forwood s.n. 1887 (K°). Measure bar equals 1 cm.

New Mexico, and extreme eastern California (Fig. 8).

**Notes.**— Even though this taxon is found in northern as well as southern areas it appears to be more abundant in southern Utah, Arizona, New Mexico, and southwestern Colorado. The long, narrow leaves and glandular pubescence are distinctive. It appears that var. *longipes* may be a transitional form between the pubescent var. *longifolia* and the glandular-pubescent var. *stansburyi*. The overlapping pattern in distribution and morphology would point to this possibility.

### *Phlox longifolia* Nutt. var. *viridis* (E. Nelson) Peabody *stat. nov.*

*Phlox viridis* E. Nelson, Wyoming Agric. Exp. Sta. Annual Rep. 9: 25. 1899. Holotype: Washington; Kittitas Co., Ellensburg, 20 May 1897, *Piper 2689* (WS°).

*P. stansburyi* (Torr.) Heller ssp. *compacta* Brand var. *puberula* (E. Nelson) Brand subvar. *viridis* (E. Nelson) Brand, Das Pflanzenreich $4^{250}$: 67. 1907.

*P. longifolia* Nutt. ssp. *viridis* (E. Nelson) Wherry, Notul. Nat. Acad. Nat. Sci. Philadelphia 87: 5. 1941.

*P. viridis* E. Nelson ssp. a-*viridis* Wherry, *pro. typ.* Morris Arb. Bull. 3: 88. 1955.

Plants short 1–3 dm, stem much branched from the base, internodes 1–2 cm long; leaves opposite, upper leaves glandular-pubescent, 16–30 mm long, 1.0–1.5 mm wide, linear; calyx glandular-pubescent, intercostal membranes usually flat; corolla tube 13–15 mm long (Fig. 9).

**Representative material.**— *Hitchcock 17409 (WTU), Peck 25922 (OSC), Davis 99-36 (IDS), Stevens 150 (BRY), Stevens 161 (BRY), Platt 157 (BRY).* 142.

**Distribution.**— Central Washington, central and southeastern Oregon, southern

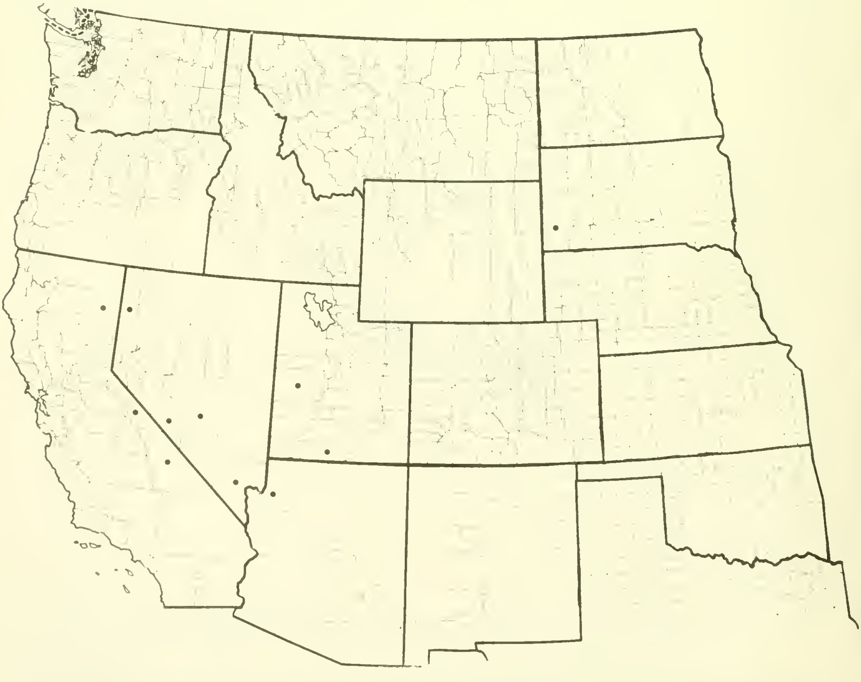

Fig. 6. Distribution of *Phlox longifolia* Nutt. var. *brevifolia* Gray over western North America.

Idaho, extreme northern Utah and Nevada (Fig. 10).

**Notes.**— Easily distinguished by its fine, narrow leaves, multiple branches, and usually congested internodes, var. *viridis* is primarily of northern distribution, extending southward along the western slope of the Rocky Mountains into northern Utah and Nevada.

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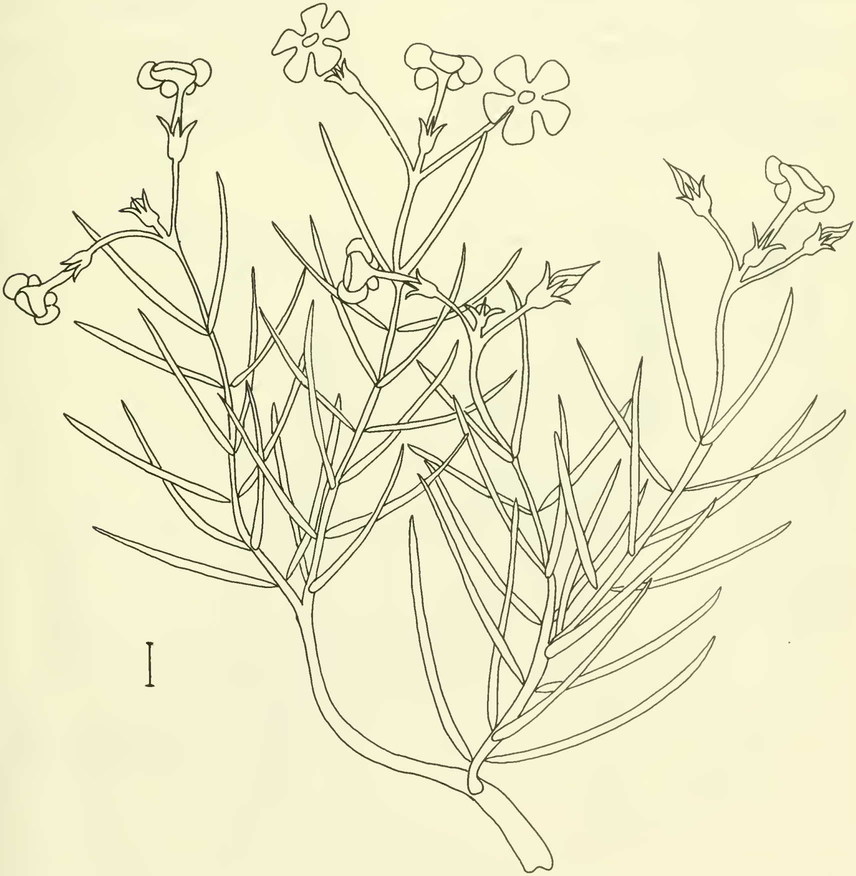

Fig. 7. *Phlox longifolia* Nutt. var. *longipes* (M. E. Jones) Peck. HOLOTYPE: Idaho, Washington Co., Weiser. M. E. Jones s.n. 28 April 1900 (POM*). Measure bar equals 1 cm.

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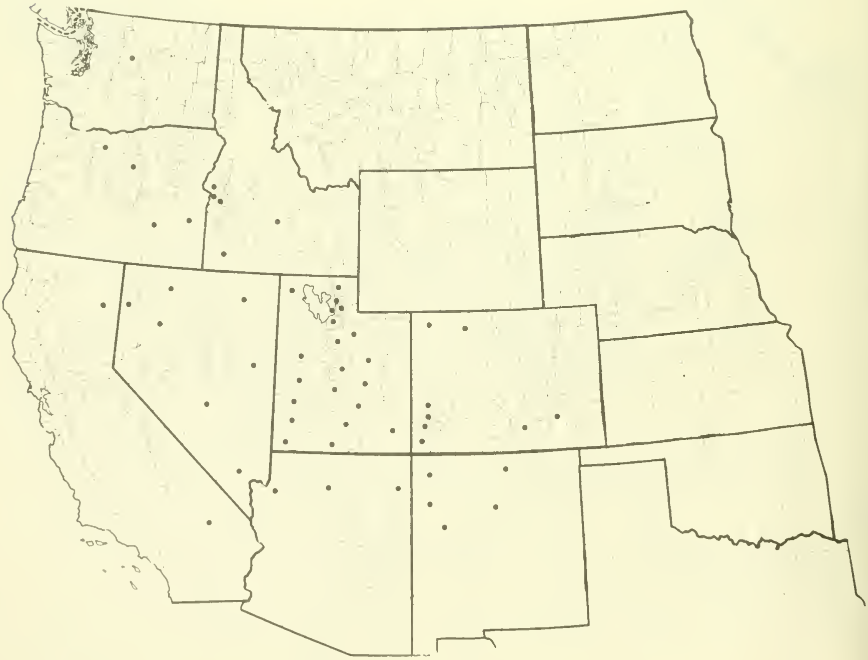

Fig. 8. Distribution of *Phlox longifolia* Nutt. var. *longipes* (M. E. Jones) Peck over western North America.

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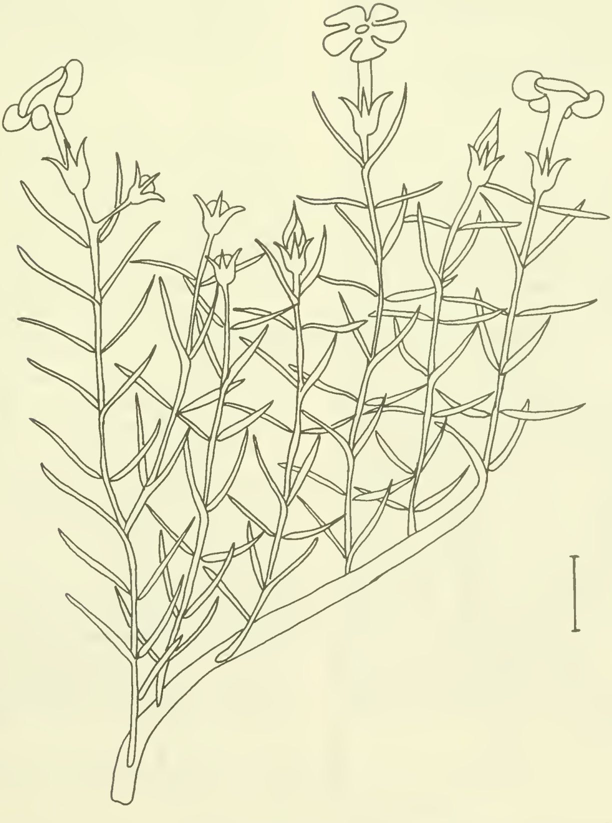

Fig. 9. *Phlox longifolia* Nutt. var. *viridis* (E. Nelson) Peabody. HOLOTYPE: Washington, Kittitas Co., Ellensburg. C. V. Piper 2689 20 May 1897 (WS°). Measure bar equals 1 cm.

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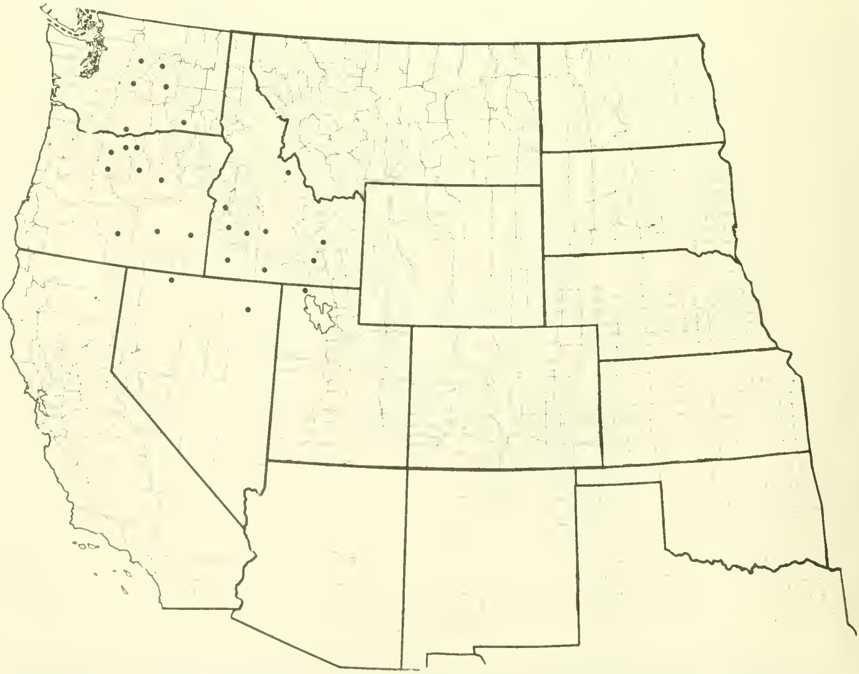

Fig. 10. Distribution of *Phlox longifolia* Nutt. var. *viridis* (E. Nelson) Peabody over western North America.

# DIATOM FLORISTICS AND SUCCESSION IN A PEAT BOG NEAR LILY LAKE, SUMMIT COUNTY, UTAH

Shobha A. Jatkar,[1] Samuel R. Rushforth,[1] and Jack D. Brotherson[1]

Abstract.—Diatoms from core samples obtained from the edge of Lily Lake, Summit County, Utah, were studied. Populations from each 15 cm of the core and niche metrics of the important species were analyzed. This study demonstrates four periods of history in the lake as mirrored by the diatom populations. The first period was mesotrophic and alkaline. This graded into an acidic, dystrophic period which in turn yielded again to a mesotrophic alkaline period. The most recent period can be characterized by a return to dystrophy.

Paleodiatomological investigations reported to date are generally based on core samples either from marine or lake sediments, and a relatively large literature is extant on this subject. However, fossil diatom studies of bogs are relatively rare. We believe the present study represents the first detailed account of fossil and living diatoms from bog samples within the Great Basin of western North America.

Most bogs in high mountain regions are formed by hydrarch succession following glaciation. Such bogs are generally acidic, highly humic, and poor in nutrients. Because of these specific features, bog floras are distinctive in biotic composition. In addition, due to high acidity and other factors, bog deposits often contain fossil or subfossil diatoms in an excellent state of preservation.

The first bog study in America was that of Lewis (1863) based on a marshy area around a shallow pond in Notch Valley in the White Mountains of New England. He observed many diatoms and desmids in his samples and drew conclusions on the relationship between the flora and geology of the area.

Patrick (1943) studied Linsely Pond, Connecticut, and observed significant changes in the diatom flora at different depths. The maximum number of diatoms, but with a low species diversity, occurred at a depth of 12 m. Species diversity increased between 12 and 9.6 m. Shallow water or littoral forms occurred in sediments from 8.4 to 6 m, but the best developed planktonic flora was observed at 5.1 m. Based on these and other observations she concluded that recent changes in the diatom flora were more or less due to the use of part of the drainage basin for agricultural purposes.

Weaver (1948) studied the diatom flora from acidic Lakeville Bog, Indiana, where he observed freshwater sponge spicules and no diatoms in sediment layers below 6.9 meters from the surface. He found maximum diatom populations in layers between 4.5 and 3.3 m and very few diatoms between 3.3 m and the surface. He found species of *Pinnularia*, *Gomphonema*, and *Eunotia* indicative of dystrophy between 4.5 and 3.3 m below the sediment surface. From these observations he inferred that during its early history, the lake was deep, clear, and poor in nutrient content. Certain sponges tolerant of oligotrophic conditions grew well in the lake during this time. Later the lake became richer in nutrients and diatoms became more prevalent. It was concluded that this lake changed from oligotrophic to dystrophic during its history.

Reimer (1961) studied the diatom flora of alkaline Cabin Creek raised bog, Indiana. He found that centric diatoms were absent and only active motile diatoms were present. According to Reimer this was possibly due to the greater adaptability of motile as opposed to nonmotile forms. He found very few *Nitzschia* species and an abundance of *Cymbella leptoceros*. From these and other observations he inferred that Cabin Creek raised bog exhibited oligotrophic conditions.

Collingsworth, Matthew, and Collins (1967) observed at Vestaburg Bog, Montcalm

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County, Michigan, a good preservation of diatoms to 14 m below the bog surface. They found a gradual increase in the diatom population from a depth of 7 m to the surface and speculated that this lake must have been oligotrophic when it originated by glaciation, later becoming eutrophic, and finally dystrophic.

Very few paleodiatomological studies have been made in Utah. Patrick (1936) collected sediment samples from various regions of the Great Salt Lake using a Musselman Peat Sampler. She identified and prepared a list of diatoms collected from each section. Based upon species present, she described the habitat of deposition for each core (especially the salinity) and inferred past ecological conditions. Patrick inferred that a freshwater lake formerly occupied the region where the Great Salt Lake occurs now. The findings of fresh and brackish water diatoms supported her conclusion that swamps existed here in Pleistocene or early Post-Pleistocene times. Lake Bonneville (the fresh water lake formerly occupying this region) gradually became more and more saline due to evaporation and lack of drainage. A marine diatom flora was never established in the lake, even though the lake went through a stage when the salinity was the same as normal marine waters. Patrick found no living diatoms in the most saline parts of the lake. However, she did obtain a few living diatoms from river deltas and areas surrounding brackish marshes where the salt concentration was not as high as in the lake proper.

Hasler and Crawford (1938) studied fossil diatoms in samples from Lake Bonneville marl sediments and found 16 genera and 27 species of diatoms. These authors drew few ecological conclusions from their data but inferred that Lake Bonneville was saline during some portion of the deposition period.

Setty (1963) studied fossil diatoms of the Pleistocene lacustrine sediments of Bonneville Basin. He found 126 taxa and presented a systematic and paleoecological discussion of these diatoms.

Bolland (1974) studied diatom deposits in a single 5 m core from Utah Lake, Utah. He observed 155 diatom taxa and studied succession through the core. By analyzing chemical and successional data, Bolland concluded that Geneva Works of United States Steel, which is located on the east shore of the lake, has had a major effect in bringing about changes in water chemistry of the lake. From these and other observations he inferred that Utah Lake is progressing from a deep water mesotrophic system to shallow water eutrophic. According to Bolland, this is mainly due to industrial development in the surrounding area and the inflow of large amounts of sewage into the lake.

Several reports have been published on geological, ecological, and floristic surveys of the Uinta Mountain region of Utah. Atwood (1909) has given an account of glaciation of the Uintas and the formation of many pothole lakes in this region. Norrington (1925) surveyed the algal flora of several mountain lakes and streams of the Wasatch and Uinta Ranges and discussed some ecological aspects of this flora. Cottam (1930) surveyed the flora of the Uinta Mountains and discussed some unusual features of this area. The algal flora of Mirror Lake was surveyed by Snow and Stewart (1939). Stutz (1951) studied some Uinta Mountain lakes from a floristic point of view. He performed analyses of pH, moisture content, and organic matter content from several lake sediments. Hayward (1952) conducted ecological studies in the Uinta Mountains and listed the characteristic plants of the ponds and surrounding zones. Christensen and Harrison (1961) studied the ecology of flowering plants and gymnosperms at Lily Lake. Vincent (1963–1964) provided information on the location, area, and depths of 100 Uinta Mountain lakes and included information on fish productivity of these lakes. Coombs (1964) made a floristic and ecological survey of the algae of the western Uinta Mountains and adjacent areas. He also gave a short geological account of the area. Palmer (1968) provided a floristic and ecological survey of the algal flora of Lily Lake. Firmage (1969) studied the flora and conifer succession of a few lakes and ponds in the Trial Lake region. Hansen (1971) published a review article on the developmental history of the Uinta Mountains. Lawson and Rushforth (1975) studied the diatom flora of the Provo River, Utah. They found 225 taxa, many of which were observed in the Uinta Mountain region.

The objectives of the present study were twofold: (1) to identify and characterize all fossil and living diatoms from Lily Lake; and (2) to determine if the pattern of diatom succession would illuminate the developmental history of this and similar Uinta Mountain bog lakes.

## STUDY AREA

Our studies were performed on samples collected from an acid *Sphagnum* bog on the edge of Lily Lake in the Uinta Mountains, Summit County, Utah. Lily Lake is representative of the many *Sphagnum* moorland lakes in the subalpine zone of these mountains. Moorland lakes, according to Tanner's (1931) system of classification, are characterized by *Sphagnum* banks, mucky bottom, and a constant surface level throughout the year. Lily Lake demonstrates all of these characteristics.

Lily Lake is about 34 km northeast of Kamas, Summit County, Utah. It is about 1 km west of the larger Trial Lake at an elevation of 3,280 m. It has a surface area of 1.2 ha and a maximum depth of 5 m (Vincent 1963–1964). Access to this lake is by foot trail from Trial Lake.

The annual snow fall in this area is around 189 cm (Whaley and Jones 1977). Snow usually persists until July and therefore the area is inaccessible for up to eight months a year. Lily Lake is surrounded by a sedge meadow which occurs in the peat soil. *Spaghnum* moss is the most important component of this meadow. Near the shore of the lake, pure stands of *Sphagnum* are common. A dense growth of the water lily *Nuphar polysepalum* (Engelm.) Green covers much of the lake surface.

Lily Lake was selected for the present investigation for several reasons. First, it is inaccessible for much of the year and is away from a main road. In addition, the area has been set aside as a botanical station for Brigham Young University. Thus, the area remains largely undisturbed by human activities, thereby avoiding soil erosion and intermixing of the fossil flora. Second, this lake represents a typical acid bog type lake (pH = 4.5 to 5.5) in the Uinta Mountains. It has acidic, organic sediments with low mineral content, and its water contains low levels of oxygen and nutrients. An excellent preservation of diatoms was noted for specimens collected down to 4 m below the bog surface. Third, due to its unique geological and geographical setting the area has been influenced by several factors, including glaciation to form lake basins, hydrarch succession to fill such basins, the admixture of southern and northern vascular floristic elements (Cottam 1930), etc. The present study was undertaken to shed light on these factors as well as to serve as a taxonomic and ecological diatom survey.

## GEOLOGY

The Uinta Mountains are in northeastern Utah (Fig. 1). They consist of a single range of peaks, extending west to east from Kamas Prairie, Utah, to the Little Snake River Valley in northwestern Colorado. This mountain range is about 240 km long and about 56 km wide. If the crest line of the range continued westward, it would cross the Wasatch range of Utah at nearly a right angle and reach the Great Bonneville Basin a few kilometers south of Salt Lake City. These two ranges are

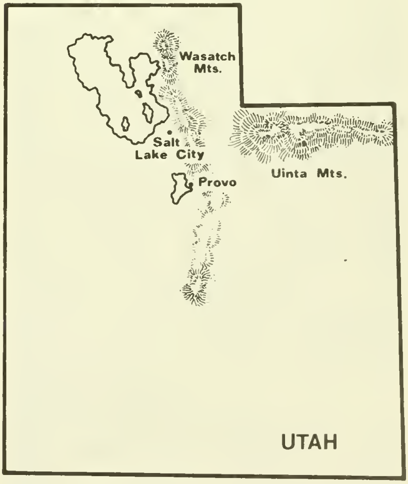

Fig. 1. Map of Utah showing the location of the Wasatch and Uinta Mountains.

separated by approximately 16 km. The strata of the Uinta Mountains are of about the same composition as the rest of the Cordillerean system to which they belong (Forrester 1937). In contrast to the remainder of the Cordillerean system (including the Rockies on the east and Pacific ranges on the west) which lie north-south, the Uinta Mountain range is oriented east-west. These mountains represent the only major east-west mountain chain in North America. The Uinta Mountains are also unique since they show an absence of igneous activity (Emmons 1907).

The lowest point of the Uinta Range is 1,816 m above sea level at Hailstone Junction. The highest point is 4,114 m at King's Peak. The range descends very abruptly at its west end and rather gradually on the east. As noted by Cottam (1930) the range has a large radiating surface which forms a highly dissected dome of great surface area. The area receives a large amount of precipitation and has relatively high temperature conditions which allow for the growth of good quality timber.

Many geologic features are evident in the Uinta Mountains due to active glaciation at different times in the history of the range. The oldest formation exposed is a Pre-Cambrian quartzite which forms the major constituent of the range. This quartzite is represented chiefly by dark red sandstones which become more and more compact toward the west. In the western half of the range, dark purplish red quartzite predominates. Interstratified layers of argillaceous shales and coarse grits are common. In the coarser beds there is considerable admixture of broken feldspar crystals. The argillaceous beds are of greenish or brownish color and are up to 30 m thick in many places. Cambrian rocks (the Tintic Quartzite) lie unconformably over the Pre-Cambrian. Comformably overlying the Tintic Quartzite is the Ophir Shale. A well-defined angular unconformity representing an extensive erosional interval occurs between Cambrian rock and the overlying Mississippian limestones. The sediments overlying the Mississippian limestones are Pennsylvanian quartzites, which in turn are overlain conformably by Park City (Permian) rocks. Triassic rocks in the Uinta sequence are represented by Woodside Shale, the Thaynes Formation, and Ankareh Shale. At the top of the Triassic sequence the Triassic-Jurassic Nugget Sandstone is present. Wherever it is exposed, the cross-bedded, wind-laid Nugget is an excellent horizon marker throughout the Uinta Range. Conformably overlying the Nugget Sandstone is the Twin Creek Formation (Jurassic). The Morrison Formation, tentatively placed in the upper Jurassic, is well exposed along the flanks of the range. Cretaceous Mesaverde, Frontier, and Mancos formations overlie the Jurassic. Wasatch (Eocene) sediments, where exposed, lie unconformably on the Mesaverde and older formations. Along much of the north flank of the range, the Green River and Bridger formations (Eocene) are the lowest Tertiary sediments exposed. Duchesne River (Oligocene) sediments are not found on the north flank of the range but are prominent along much of the south slope. Pleistocene glacial drift and debris cover much of the underlying structure in the Uinta Range, and it is often difficult to separate these late deposits from older Tertiary sediments.

As reported by Atwood (1909) all the larger canyons have a characteristic U-shape due to glaciation. Their upper portions have been well cleaned by the ice, but the middle and lower portions often contain heavy morainic deposits. The floors of the basin in which the ice formed are all above 2,743 m but there is no sign of ice on the flanks of the range even at the 3,048 m level.

Atwood (1909) also presented evidence of at least two separate epochs of glaciation. The earlier epoch was presumably the longer because the ice of that epoch was thicker and extended farther down the canyons. About 30 major glaciers occurred in this earlier epoch and about 39 in the later epoch.

Glaciation often has a great influence on drainage systems. The hundreds of lakes and marshes in the Uinta Mountains indicate that the drainage has been greatly modified by the ice. The area is drained by many streamlets which feed into the Bear River draining northward, the Weber River westward, the Provo River southwest, and the Duchesne River and Rock Creek southeast. Among these mountains, there are now more than 550 glacial lakes (Atwood 1909). Lily Lake is one of these lakes. There were many more lakes at the close of glaciation, but since then succession has progressed to completion in many to create meadows.

## Methods

Samples were collected in October 1975 from the northeast side of Lily Lake using a peat borer. A 3.76 m core was taken and subsampled every 15 cm. Two samples of the living flora were also collected, including one from the water of the lake and the other from the mucky bottom and moss at the edge of the lake. All samples were examined in the field and their color and organic content recorded.

The samples were transferred to clean glass bottles, labeled, and sealed. Samples were brought to the laboratory and refrigerated until further processing. A small quantity of material from each sample was boiled in concentrated nitric acid, and permanent diatom slides were prepared by standard methods (St. Clair and Rushforth 1977). Diatoms were mounted in Hyrax mounting medium.

Diatoms were identified under 1000X oil immersion using a Zeiss RA microscope. Counts of at least 400 diatom frustules were made for all sample depths except for sample Number 1 from the bottom of the core, which contained few diatoms.

The absolute and relative density for each species at each sample depth was computed. Species diversity values were also calculated for each sample using the Shannon-Weaver (Shannon and Weaver, 1963) formula. Regression analyses of floral diversity versus sample depth were conducted using standard statistical methods.

Similarity indices between all samples in the study were calculated (Ruzicka 1958), and cluster analysis (Sneath and Sokal 1963) based upon similarity indices was performed.

The most important species in each of the groups delineated by cluster analysis were determined using PxF indices (percent frequency times average percent density; Warner and Harper 1972).

A list of prevalent species was prepared by selecting species present in 30 percent or more of the samples.

Niche breadth and niche overlap values were obtained (Colwell and Futuyma 1971) for the prevalent species. A cluster analysis based on the niche overlap of these species was then performed (Cody 1974).

Where possible, the pH preference and saprobien spectrum for the diatoms encountered in this study were determined. This information was tabulated and plotted.

## Results and Discussion

### Taxonomy

The 157 diatom taxa encountered in this study are arranged systematically in the following section. Measurements of length and width (or diameter), number of striae, and number of costae are given for each taxon when applicable. A brief discussion of the distribution and maximum relative frequency of each taxon is given. References to detailed descriptions for each taxon are provided.

The slides upon which these determinations were made have been deposited in the Brigham Young University collections.

### Coscinodiscaceae

***Melosira dickiei*** **(Thwait.) Kützing:** Valve diameter 6–15 ; punctae scattered in central region. (Hustedt 1930:86). Frustules were present throughout the core though their percent frequency was low. It constituted 2 percent of the total diatom population from 150 to 135 cm.

***Melosira distans*** **(Ehr.) Kützing:** Valve diameter 12–17 μm; striae punctate, 10–15 in 10 μm (Hustedt 1930:93). It was scattered in core samples only from 360 to 225 cm. The maximum number of frustules was observed in samples from 360 to 330 cm.

***Melosira distans*** **var. *pfaffiana*** **(Reinsch) Grunow:** Valve in girdle view 7 μm long, 6 μm wide, striae 15 in 10 μm. (Hustedt 1930:93). Frustules were very rare and unevenly distributed in the core.

***Melosira granulata*** **(Ehr.) Ralfs:** Valve in girdle view 7–17 μm long, 5–16 μm wide; striae 10–15 in 10 μm; spines 10 in 10 μm (Hustedt 1930:87). Though frustules were scattered throughout the core, they were most common from 180 to 75 cm. They exhibited great variation in size and especially in size of punctae.

***Melosira italica* (Ehr.) Kützing:** Valve in girdle view 10–14 μm long, 10–15 μm wide; striae 18–20 in 10 μm (Hustedt 1930:91). Frustules were present from 360 to 345 cm but only very rarely observed in samples from other depths. It constituted 4.2 percent of the diatom population at 345 cm.

***Cyclotella antiqua* W. Smith:** Valve diameter 22 μm; striae 14–20 in 10 μm (Hustedt 1930:102). Frustules were only rarely observed and usually broken. A single entire specimen was observed in a sample from 270 cm.

***Cyclotella catenata* Brun:** Valve diameter 17 μm; striae about 10 in 10 μm (Hustedt 1930:108). A single frustule was observed at 120 cm.

***Cyclotella comensis* Grunow:** Valve diameter 8 μm; striae 20 in 10 μm (Hustedt 1930:102). Only one unbroken specimen was observed at 105 cm.

***Cyclotella kützingiana* Thwaites:** Valve diameter 14–15 μm; striae 9–10 in 10 μm (Hustedt 1930:98). Frustules were present from 210 to 45 cm. The maximum number was observed in samples from 180 cm and 105 cm where they constituted 2.6 percent of the diatom population.

***Cyclotella meneghiniana* Kützing:** Valve diameter 8–8.5 μm; striae 14–20 in 10 μm (Hustedt 1930:100). Frustules were very rare and were observed only in samples from 280 to 255 cm. Their maximum percent frequency was 0.4 percent at 255 cm.

***Cyclotella striata* (Kützing) Grunow:** Valve diameter 25 μm; striae 8–10 in 10 μm (Hustedt 1930:101). A single specimen was observed at 150 cm.

***Stephanodiscus astrea* var. *minutula* (Kütz.) Grunow:** Valve diameter 12–18 μm; striae up to 15 in 10 μm (Hustedt 1930:110). It was observed in samples from 360 to 135 cm. The maximum number of frustules (1.2 percent) was observed at 180 cm.

***Stephanodiscus dubius* (Fricke) Hustedt:** Valve diameter 28–35 μm; striae 8–12 in 10 μm (Hustedt 1930:109). Frustules were present from 180 to 90 cm. The maximum number was observed in samples from 135 cm, where they constituted 2 percent of the diatom population.

***Stephanodiscus niagarae* (Ehr.) Grunow:** Valve diameter 28–38 μm; striae 10–15 in 10 μm (Cleve-Euler 1951:53). Frustules were very rarely observed. The maximum number was found in samples from 180 cm, where they constituted 0.6 percent of the diatom population.

***Coscinodiscus odontodiscus* Grunow:** Valve diameter 26–27 μm; striae 16–17 in 10 μm (Cleve-Euler 1951:59). Frustules were observed from 210 to 105 cm. The maximum relative density was 0.6 percent in samples from 120 cm.

***Coscinodiscus rothii* (Ehr.) Grunow:** Valve diameter 27 μm; aerolae about 16 in 10 μm (Hustedt 1930:112). A single specimen was observed at 120 cm.

### FRAGILARIACEAE

***Tabellaria fenestrata* (Lyngb.) Kützing:** Valve 25–51 μm long; 5–7 μm wide; striae 20–22 in 10 μm (Hustedt 1930:122). It was observed very frequently in samples from throughout the core. The maximum relative density was 25.7 percent at 225 cm and the lowest was 0.2 percent at 105 cm.

***Tabellaria flocculosa* (Roth) Kützing:** Valve 13–17 μm long; 6–8 μm wide; striae about 18 in 10 μm (Hustedt 1930:123). Frustules were observed from 210 to 30 cm and also in surface samples. The maximum relative density was 5.6 percent at 30 cm.

***Diatoma anceps* (Ehr.) Kirchner:** Valve 24 μm long by 4–5.5 μm wide; costae 5 in 10 μm; striae 15–20 in 10 μm (Patrick and Reimer 1966:106). It was observed as an entire specimen only once at 270 cm.

***Diatoma hiemale* var. *mesodon* (Ehr.) Grunow:** Valve 14–15 μm long by 7–8 μm wide; costae 3–4 in 10 μm; striae about 18 in 10 μm (Patrick and Reimer 1966:108). Frustules were very rarely observed in scattered samples in the core.

***Diatom vulgare* Bory:** Valve 43–48 μm long by 12–14 μm wide; costae 6–8 in 10 μm; striae about 14 in 10 μm (Patrick and Reimer 1966:109). It was observed in samples from 180 to 120 cm. The maximum occurrence was from 180 cm to 150 cm, where it constituted 3.6 percent and 5.2 percent, respectively, of the total diatom population.

***Diatoma vulgare* var. *breve* Grunow:** Valve 28–32 μm long by 12 μm wide; costae 7–9 in 10 μm; striae 1–2 between costae (Patrick and Reimer 1966:110). Frustules were observed in samples from 150 cm only.

***Meridion circulare* (Grev.) Agardh:** Valve 26–28 μm long by 5–6 μm wide; costae 3–5 in 10 μm; striae 16–18 in 10 μm (Patrick and Reimer 1966:113). One or two specimens were observed in modern plankton samples.

***Fragilaria brevistriata* Grunow:** Valve 20–23 μm long by 3–3.5 μm wide; striae 14 in 10 μm (Patrick and Reimer 1966:128). Frustules were scattered in samples from 240 to 15 cm. The maximum relative density of 2.8 percent was from 150 cm.

***Fragilaria brevistriata* var. *inflata* (Pant.) Hustedt:** Valve 9–15 μm long by 4–5 μm wide; striae 10–14 in 10 μm (Patrick and Reimer 1966:129). Frustules were scattered in samples from 360 to 75 cm. Their maximum relative density of 9 percent was at 135 cm.

***Fragilaria constricta* Ehrenberg:** Valve 40 μm long by 8 μm wide; striae 18 in 10 μm (Patrick and Reimer 1966:122). Frustules were very rarely observed in the sample from 165 cm.

***Fragilaria constricta* f. *stricta* (A. Cl.) Hustedt:** Valve 24–28 μm long by 11–13 μm wide; striae 16–18 in 10 μm (Patrick and Reimer 1966:123). Frustules were rare and observed only from 150 cm.

***Fragilaria construens* var. *venter* (Ehr.) Grunow:** Valve 7–10 μm long by 4–5 μm wide; striae 14–16 in 10 μm (Patrick and Reimer 1966:126). It was abundant throughout the core except in modern plankton samples. The maximum relative density of 18.4 percent was from 240 cm.

***Fragilaria crotonensis* Kitton:** Valve 43–45 μm long by 2–3 μm wide; striae 14 in 10 μm (Patrick and Reimer 1966:121). Frustules were rarely observed in samples from 360 to 270 cm. It constituted a maximum of only 0.2 percent of the diatom population.

***Fragilaria intermedia* Grunow:** Valve 39 μm long by 8 μm wide; striae 11–12 in 10 μm (Hustedt 1930:139). A single frustule was observed at 150 cm.

***Fragilaria lapponica* Grunow:** Valve 19–24 μm long by 5–6 μm wide; striae 9–10 in 10 μm (Patrick and Reimer 1966:130). It was observed from 360 to 75 cm.

***Fragilaria leptostauron* (Ehr.) Hustedt:** Valve measurements not obtained (Patrick and Reimer 1966:124). It was observed as a single specimen in a sample from 135 cm.

***Fragilaria virescens* Ralfs:** Valve 13–35 μm long by 5–10 μm wide; striae 14–22 in 10 μm (Patrick and Reimer 1966:119). Frustules were abundant in samples from all levels except from 105 to 75 cm and in the modern plankton. The maximum percent relative density of 18.4 percent was observed in samples from 195 cm.

***Synedra amphicephala* Kützing:** Valve 22 μm long by 3 μm wide; striae 16 in 10 μm (Hustedt 1930:156). A single frustule was observed at 270 cm.

***Synedra rumpens* Kützing:** Valve 38 μm long by 2 μm wide; striae 16–18 in 10 μm (Hustedt 1930:156). A single frustule was observed at 270 cm.

***Synedra tenera* W. Smith:** Valve 46–47 μm long by 3–3.5 μm wide; striae 22–24 in 10 μm (Patrick and Reimer 1966:137). Frustules were scattered in samples from 180 to 75 cm. They constituted a maximum of 1.2 percent of the diatom population from 135 cm.

***Synedra ulna* (Nitzsch) Ehrenberg:** Valve 6 μm wide; striae 10 in 10 μm (Patrick and Reimer 1966:148). No entire frustules were found, although fragments were observed in samples from 90 cm.

***Synedra* species 1:** Valve curved, 80–100 μm long, 9 μm wide; axial area distinct, linear, hyaline; central area absent; striae 18 in 10 μm, parallel throughout valve. Specific identification of this taxon was not possible and no entire specimens were observed. Fragments were scattered from 315 to 195 cm with very low abundance.

***Synedra* species 2:** Valve 26–35 μm long by 2–5 μm wide; striae 14–18 in 10 μm. Frustules were similar to *S. capitata* in shape but were smaller. They were scattered in samples from 240 to 195 cm, where they constituted a maximum of 0.2 percent of the total diatom population.

### EUNOTIACEAE

***Eunotia arcus* Ehrenberg:** Valve 12–35 μm long by 4–5 μm wide; striae 13–14 in 10 μm (Patrick and Riemer 1966:212). Frustules were observed in samples only from the 210 cm level.

***Eunotia arcus* var. *uncinata* (Ehr.) Grunow:** Valve 21 μm long by 5 μm wide; striae about 14 in 10 μm (Patrick and Reimer 1966:213). It was observed as a single specimen in a sample from 270 cm.

***Eunotia curvata* (Kütz.) Largest.:** Valve 30–32 μm long by 2–4μm wide; striae 14–15 in 10 μm (Patrick and Reimer 1966:189). Frustules were scattered throughout the core. The maximum relative density of 6 percent was observed in modern samples.

***Eunotia exigua* (Bréb. *ex* Kutz.) Rabenhorst:** Valve 12–35 μm long by 4–5 μm wide; striae 18–20 in 10 μm (Patrick and Reimer 1966:215). It was common throughout the core and was also observed in modern samples. Its maximum relative density of 18.4 percent was observed from 60 cm.

***Eunotia hexaglyphis* Ehrenberg:** Valve 35–45 μm long by 8 μm wide; striae 16 in 10 μm (Patrick and Reimer 1966:203). It was observed from 225 to 195 cm only. Its maximum relative density of 3.2 percent was from 195 cm.

***Eunotia incisa* W. Smith *ex* Greg.:** Valve 30–33 μm long by 5–5.5 μm wide; striae about 19 in 10 μm (Patrick and Reimer 1966:208). It was observed in three distinct zones from 285 to 195 cm, 60 to 45 cm, and in modern samples. In addition, a single frustule was observed at 360 cm. The maximum relative density was 2.2 percent at 195 cm.

***Eunotia lapponica* Grunow *ex* A. Cleve:** Valve about 50 μm long by 6 μm wide; striae 20 in 10 μm (Patrick and Reimer 1966:192). Frustules were observed from 225 to 165 cm and from 120 to 15 cm. The maximum numbers were observed from 30 cm, where they constituted 9.6 percent of total diatom population.

***Eunotia maior* (W. Sm.) Rabenhorst:** Valve 80–168μm long by 8–14 μm wide; striae 9–10 in 10 μm (Patrick and Reimer 1966:196). Specimens were rare in the sample from 180 cm.

***Eunotia naegelii* Migula:** Valve 57 μm long by 3 μm wide; striae 18 in 10 μm (Patrick and Reimer 1966:190). A single frustule was observed in a sample from 60 cm.

***Eunotia nymanniana* Grunow:** Valve 22 μ long by 3 μm wide; striae 14 in 10 μm (Patrick and Reimer 1966:214). A single specimen was observed in a sample from 150 cm.

***Eunotia pectinalis* var. *minor* (Kütz.) Rabenhorst:** Valve 30–32 μm long by 5–6 μm wide; striae 16–18 in 10 μm (Patrick and Reimer 1966:207). *E. pectinalis* var. *minor* was observed at 285 cm and from 60 to 45 cm. The maximum relative density of 2 percent was observed at 60 cm.

***Eunotia praerupta* var. *bidens* (Ehr.) Grunow:** Valve 60 μm long by 12–13 μm wide; striae 12 in 10 μm (Patrick and Reimer 1966:194). Frustules were observed only at 210 cm and 60 cm, where they constituted 0.8 percent and 0.2 percent of the total diatom population respectively.

***Eunotia praerupta* var. *inflata* Grunow:** Valve 33–53 μm long by 10–16 μm wide; striae 7–9 in 10 μm (Patrick and Reimer 1966:194). Frustules were scattered in samples from 210 to 15 cm. They constituted 4 percent of the flora at 30 cm.

***Eunotia septentrionalis* Oestrup:** One broken specimen was observed at 135 cm (Patrick and Reimer 1966:212).

***Eunotia serra* var. *diadema* (Ehr.) Patrick:** Valve 30–45 μm long by 11–18 μm wide; striae 11–12 in 10 μm (Patrick and Reimer 1966:201). It was observed mainly from 270 to 180 cm. A single frustule was found from 75 cm. A maximum relative density of 3.4 percent was observed from 195 cm.

***Eunotia suecica* A. Cleve:** Valve 27 μm long by 9 μm wide; striae 14 in 10 μm. (Patrick and Reimer 1966:199). One specimen was observed from 210 cm.

***Eunotia valida* Hustedt:** Valve 57–70 μm long by 5–6 μm wide; striae 12–14 in 10 μm (Patrick and Reimer 1966:192). It was scattered in samples from 285 to 30 cm and was also in the modern plankton. A maximum relative density of 5.2 percent was observed from 210 cm.

***Eunotia vanheurckii* Patrick:** Valve 35–38 μm long by 9–10 μm wide; striae 16–20 in 10 μm (Patrick and Reimer 1966:210). It was scattered in lower samples from 345 to 195 cm. A few frustules were observed from 60 cm. A maximum relative density of 1.6 percent was observed from 195 cm.

***Eunotia vanheurckii* var. *intermedia* (Krasske *ex* Hust.) Patrick:** Valve 15–16 μm long by 3–4 μm wide; striae 16 in 10 μm (Patrick and Reimer 1966:211). It was observed in samples from 285 to 270 cm.

### ACHNANTHACEAE

***Cocconeis pediculus*** **Ehrenberg:** Valves 25–26 µm long by 17–21 µm wide; striae 19–20 in 10 µm (Patrick and Reimer 1966:240). Frustules were observed from 360 cm and from 150 to 135 cm. At 150 cm it constituted 2.2 percent of total diatom population.

***Cocconeis placentula*** **var.** ***eugylpta*** **(Ehr.) Cleve:** Valve 13–26 µm long by 8–20 µm wide; striae 19–24 in 10 µm (Patrick and Reimer 1966:241). It was observed from 180 to 90 cm. It had a maximum relative density of 4.8 percent from 150 cm. Two frustules were additionally observed in the modern plankton sample.

***Achnanthes biasolettiana*** **Kützing:** Valve 12–12.5 µm long by 4 µm wide; striae 18 in 10 µm (Hustedt 1930:199). A few frustules were observed at 120 cm.

***Achnanthes conspicua*** **A. Mayer:** Valve 7–8 µm long by 4 µm wide; striae 18 in 10 µm on raphe valve (Hustedt 1930:202). Frustules were observed only from 270 cm, where they constituted 1.4 percent of total diatom population.

***Achnanthes delicatula*** **Kützing:** Valve 16–17 µm long by 5–5.5 µm wide; striae 15–17 in 10 µm on raphe valve (Hustedt 1930:202). Frustules were observed only from 240 cm, where they constituted 0.7 percent of the total diatom population.

***Achnanthes linearis*** **f.** ***curta*** **H. L. Smith:** Valve about 10 µm long by 2.5–3.5 µm wide; striae about 25 in 10 µm (Patrick and Reimer 1966:252). Frustules were scattered in samples from 360 to 225 cm, 150 cm, 90 cm, and the extant plankton. The maximum relative density of 7.7 percent for this taxon was observed from 255 and 240 cm.

***Achnanthes linearis*** **var.** ***pusilla*** **Grunow:** Valve 15–16 µm long by 3.5–5 µm wide; striae 22–24 in 10 µm (Patrick and Reimer 1966:252). It was observed only from 360 to 225 cm. The maximum relative density of 9.1 percent was observed at 315 cm.

***Achnanthes minutissima*** **Kützing:** Valve 9–11 µm long by 2.5 µm wide; striae very fine (Hustedt 1930:198). Frustules were observed at 120 cm.

***Achnanthes minutissima*** **var.** ***cryptocephala*** **Grunow:** Valve 13–18 µm long by 2–3.5 µm wide; striae very fine. (Hustedt 1930:198). Frustules were observed only from 270 to 225 cm. The maximum relative density was 7.9 percent at 240 cm.

### NAVICULACEAE

***Mastogloia elliptica*** **Agardh:** Valve 25–38 µm long by 10 µm wide; striae about 16 in 10 µm (Hustedt 1930:217). *M. elliptica* frustules were rare in samples from 60 cm.

***Frustulia rhomboides*** **(Ehr.) de Toni:** Valve 120–125 µm long by 20–22 µm wide; striae 20–25 in 10 µm (Patrick and Reimer, 1966:306). *F. rhomboides* frustules were scattered in the deeper section of the core from 360 cm to 165 cm. This taxon constituted 3.6 percent of the total diatom population from 300 cm.

***Frustulia rhomboides*** **var.** ***capita*** **(A. Mayer) Patrick:** Value 39–45 µm long by 10–11 µm wide; striae about 30 in 10 µm (Patrick and Reimer 1966:307). Frustules of this taxon were scattered throughout the core. A maximum relative density of 16.2 percent occurred in the surface sample.

***Frustulia rhomboides*** **var.** ***crassinervia*** **(Bréb.** ***ex*** **W. Sm.) Ross:** Valve 45–46 µm long by 10–10.5 µm wide; striae very fine, unresolvable (Patrick and Reimer 1966:307). It was observed in samples from 180 to 15 cm and also in the surface sample. A maximum frequency of 18.8 percent was from 90 cm.

***Caloneis limosa*** **(Kütz.) Patrick:** Valve 55–70 µm long by 10–12 µm wide; striae 16–20 in 10 µm (Patrick and Reimer 1966:587). One or two specimens of this taxon were observed from 360 cm.

***Neidum bisulcatum*** **(Lagerst.) Cleve:** Valve 50–70 µm long by 9–12 µm wide; striae 26–30 in 10 µm (Patrick and Reimer 1966:397). A few specimens of *N. bisulcatum* were observed from 360 cm.

***Neidium iridis*** **(Ehr.) Cleve:** Valve 50–80 µm long by 14–20 µm wide; striae about 20 in 10 µm (Patrick and Reimer 1966:386). It was only in samples from the lower section of the core (360 to 225 cm). A maximum relative density of 2 percent was observed in samples from 360 cm.

***Neidium iridis*** **var.** ***amphigomphus*** **(Ehr.) A. Mayer:** Valve 45–122 µm long by 16–25 μm wide; striae 16–18 in 10 μm (Patrick and Reimer 1966:387). It was observed mainly from the deeper section of the core (345 to 210 cm). A maximum relative density of 3.2 percent was observed from 240 cm. A few frustules were from 30 cm, 15 cm, and the modern plankton sample.

***Neidium iridis* var. *ampliatum* (Ehr.) Cleve:** valve 35–85 μm long by 12–20 μm wide; striae about 20 in 10 μm (Patrick and Reimer 1966:388). It was observed from 330 and 315 cm where it constituted about 3.5 percent of the diatom population. A few frustules were from 255 cm and in the extant plankton.

***Diploneis elliptica* (Kütz.) Cleve:** Valve 37 μm long by 25 μm wide; costae 8–9 in 10 μm; alveoli in single row between costae (Patrick and Reimer 1966:414). It was observed only from 165 cm and 105 cm, where it occurred as single specimens.

***Diploneis interrupta* (Kütz.) Cleve:** Valve 55 μm long by 8–9 μm wide; costae 8 in 10 μm (Patrick and Reimer 1966:416). A single entire frustule was observed from 75 cm.

***Diploneis smithii* var. *dilatata* (M. Perag.) Boyer:** Valve 36–37 μm long by 18–18.5 μm wide; costae 10 in 10 μm; double row of alveoli between costae (Patrick and Reimer 1966:411). Frustules were observed only from 180 cm and 135 cm. The maximum relative density of 1.2 percent was observed from 135 cm.

***Stauroneis anceps* Ehrenberg:** Valve about 70 μm long by about 14 μm wide; striae 18 in 10 μm (Patrick and Reimer 1966:361). It was observed mostly from 360 to 135 cm. The maximum frequency of 1.6 percent was observed from 345 cm.

***Stauroneis anceps* f. *gracilis* Rabenhorst:** Valve to 67 μm long by up to 14 μm wide; striae very fine (Patrick and Reimer 1966:361). It was observed only in the deeper section of the core (from 360 to 240 cm). It constituted 0.9 percent of the diatom population from 315 cm and 240 cm.

***Stauroneis kriegeri* Patrick:** Valve 12–23 μm long by 3 μm wide; striae about 26–28 in 10 μm (Patrick and Reimer 1966:362). Very few specimens were observed only from the upper core.

***Stauroneis phoenicenteron* (Nitz.) Ehrenberg:** Valve 155–157 μm long by 25–26 μm wide; striae 14–15 in 10 μm (Patrick and Reimer 1966:359). It was observed from 330 to 285 cm and from 210 to 195 cm. This diatom constituted 1.2 percent of the total population from 285 cm. A single frustule was in the extant plankton.

***Anomoeoneis costata* (Kütz.) Hustedt:** Valve 75 μm long by 25 μm wide; striae 16 in 10 μm (Patrick and Reimer 1966:376). Only one or two specimens were observed from 90 cm.

***Anomoeoneis serians* var. *acuta* Hustedt:** Valve 29–40 μm long by 7.5–8 μm wide; striae 26–28 in 10 μm (Patrick and Reimer 1966:378). This taxon was observed in extant samples only where it constituted 4.6 percent of the diatom population.

***Anomoeoneis serians* var. *brachysira* (Bréb. *ex* Kütz.) Hustedt:** Valve 15–32 μm long by 5–6.5 μm wide; striae 24–30 in 10 μm (Patrick and Reimer 1966:379). Frustules were abundant throughout the core. A maximum frequency of 16.4 percent was observed from 30 cm.

***Anomoeoneis vitrea* (Grun.) Ross:** Valve 25–32 μm long by 5–6 μm wide; striae 30 or finer in 10 μm (Patrick and Reimer 1966:380). Frustules were very common in deeper parts of the core (from 360 to 225 cm). This taxon constituted 3.2 percent of the flora from 225 and 240 cm.

***Navicula aikenensis* Patrick:** Valve 18–25 μm long by 5–6 μm wide; striae about 16 in 10 μm (Patrick and Reimer 1966:473). It was observed only from 360 to 225 cm. A maximum relative density of 1.2 percent was observed from 285 cm.

***Navicula angusta* Grunow:** Valve 55–62 μm long by 5–7 μm wide; striae 12–14 in 10 μm (Patrick and Reimer 1966:514). It was observed only from 285 cm and from 240 cm to 225 cm. A maximum relative density of 1.4 percent was observed from 285 cm.

***Navicula höfleri* Cholnoky:** Valve 31–32 μm long by 8–8.5 μm wide; striae very fine (Hustedt 1961–1966:97). Frustules were scattered throughout the core. A maximum relative density of 9.6 percent was observed from 15 cm.

***Navicula mutica* Kützing:** Valve 13–15 μm long by 5–6 μm wide; striae about 20 in 10 μm (Patrick and Reimer 1966:454). It was observed from 195 to 45 cm. A maximum relative density of 7.2 percent was observed from 135 cm.

***Navicula mutica* var. *cohnii* (Hilse) Grunow:** Valve 14–15 μm long by 6–7 μm wide; striae 16–18 in 10 μm (Patrick and Reimer 1966:454). It was observed rarely at 285 cm.

***Navicular mutica* var. *undulata* (Hilse) Grunow:** Valve 9–16 μm long by 5–7 μm wide; striae 18–20 in 10 μm (Patrick and Reimer 1966:456). It was observed only at 240 cm and from 105 to 90 cm. Single frustules were observed at each level.

***Navicula pelliculosa* (Bréb.) Hilse:** Valve 6 μm long by 4 μm wide; striae very fine (Hustedt 1930:287). One specimen was observed at 105 cm.

***Navicula pseudoscutiformis* Hustedt:** Valve 12–13 μm long by 10 μm wide; striae 20–22 in 10 μm (Patrick and Reimer 1966:451). It was observed from 285 to 240 cm. A maximum relative density of 2 percent was observed from 255 cm.

***Navicula pupula* var. *rectangularis* (Greg.) Grunow:** Valve 25–37 μm long by 8–9 μm wide; striae 20 in 10 μm (Patrick and Reimer 1966:497). Frustules were scattered from 360 to 90 cm and a few were observed from surface samples. A maximum relative density of 19.4 percent was observed from 345 cm.

***Navicula radiosa* Kützing:** Valve 70–83 μm long by 10–12 μm wide; striae 12–13 in 10 μm (Patrick and Reimer 1966:509). It was observed mostly in deeper samples (360 to 225 cm). A few frustules were scattered in some of the upper and the extant samples. A maximum frequency of 5.6 percent was observed from 270 cm.

***Navicula subtilissima* Cleve:** Valve 20–28 μm long by 4–6 μm wide; striae very fine (Patrick and Reimer 1966:483). Frustules were scattered throughout the core but primarily in the upper strata. A maximum relative density of 21 percent was observed from 150 cm.

***Navicula longirostris* Hustedt:** Valve 18–19 μm long by 3–3.5 μm wide; striae very fine (Hustedt 1930:285). Frustules occurred only from 315 to 240 cm. A maximum relative density of 2.5 percent was observed at 315 and 285 cm.

***Pinnularia abaujensis* (Pant.) Ross:** Valve 60 μm long by 12 μm wide; striae 13–14 in 10 μm (Patrick and Reimer 1966:612). Frustules were observed rarely from 285–270 cm, from 210 cm, and from 90 cm. A maximum relative density of 0.6 percent was observed from 90 cm.

***Pinnularia abaujensis* var. *rostrata* (Patr.) Patrick:** Valve 60–62 μm long by 11–12 μm wide; striae to 14 in 10 μm (Patrick and Reimer 1966:614). Only one or two frustules were observed from 270 cm.

***Pinnularia biceps* Greg.:** Valve 39–71 μm long by 8–10 μm wide; striae 10–15 in 10 μm (Patrick and Reimer 1966:599). It was present throughout the core. A maximum relative density of 20.4 percent was observed from 330 cm.

***Pinnularia borealis* Ehrenberg:** Valve 32–44 μm long by 8.5–10 μm wide; striae 5–6 in 10 μm (Patrick and Reimer 1966:618). Frustules were observed from 210 cm and from 150 to 45 cm. A maximum relative density of 2.4 percent was observed from 135 cm.

***Pinnularia braunii* (Grun.) Cleve:** Valve 35–37 μm long by 8–9 μm wide; striae 12 in 10 μm (Patrick and Reimer 1966:594). It occurred only from 360 cm and 345 cm. A maximum relative density of 1.7 percent was observed from 360 cm.

***Pinnularia brebissonii* (Kütz.) Rabenhorst:** Valve 42–75 μm long by 7–11 μm wide; striae 8–14 in 10 μm (Patrick and Reimer 1966:614). A few specimens of *P. brebissonii* were observed at 360 cm and 255 cm.

***Pinnularia dactylus* Ehrenberg:** Valve 230–235 μm long by 28–30 μm wide; striae 4–5 in 10 μm (Patrick and Reimer 1966:632). Single frustules were observed from 285 cm to 255 cm only.

***Pinnularia divergens* W. Smith:** Valve 65 μm long by 15 μm wide; striae 12 in 10 μm (Hustedt 1930:323). It was observed at 345 cm.

***Pinnularia gibba* Ehrenberg:** Valve 60–100 μm long by 10–12 μm wide; striae 8–12 in 10 μm (Hustedt 1930:327). Frustules were observed from 360 to 210 cm. A maximum relative density of 3.2 percent was observed from 285 cm.

***Pinnularia mesolepta* f. *angusta* Cleve:** Valve 26–60 μm long by about 5–7.5 μm wide; striae 12–20 in 10 μm (Hustedt 1930:319). A few frustules were observed at 360 cm.

***Pinnularia microstauron*** **(Ehr.) Cleve:** Valve 52–63 μm long by 10–12 μm wide; striae 9–13 in 10 μm (Patrick and Reimer 1966:597). It was observed in all strata. At 45 cm these frustules constituted 46 percent of the total diatom population.

***Pinnularia molaris*** **Grunow:** Valve 30 μm long by 7 μm wide; striae 14 in 10 μm (Hustedt 1930:316). A few frustules were observed in the extant plankton sample.

***Pinnularia nobilis*** **(Ehr.) Ehrenberg:** Valve 280–282 μm long by about 30 μm wide; striae to 7 in 10 μm (Patrick and Reimer 1966:638). Single frustules of *P. nobilis* were observed from 165 cm and 120 cm.

***Pinnularia platycephala*** **(Ehr.) Cleve:** Valve 77 μm long by 18 μm wide; striae 10 in 10 μm (Hustedt 1930:324). A single frustule was observed at 360 cm.

***Pinnularia subsolaris*** **(Grun.) Cleve:** Valve 75 μm long by 15 μm wide; striae 10 in 10 μm (Hustedt 1930:322). Frustules were observed only from 360 and 345 cm. A maximum frequency of 0.5 percent was observed from 360 cm.

***Pinnularia viridis*** **(Nitzsch) Ehrenberg:** Valve 120–175 μm long by 21–30 μm wide; striae 5–9 in 10 μm (Patrick and Reimer 1966:639). It was scattered in the deeper section of the core (from 360 to 210 cm only). A maximum relative density of 7.4 percent was observed from 210 cm.

***Pinnularia viridis*** **var. *commutata*** **(Grun.) Cleve:** Valve 42–90 μm long by 9–17 μm wide; striae 9–14 in 10 μm (Patrick and Reimer 1966:640). It was observed at 360 cm.

***Pinnularia viridis*** **var. *minor*** **Cleve:** Valve 85–100 μm long by about 18 μm wide; striae 8–9 in 10 μm (Patrick and Reimer 1966:641). It was observed from 135 to 15 cm. A maximum relative density of 12.2 percent was observed from 75 cm.

***Pinnularia*** **species 1:** Valve 25–35 μm long by 9–10 μm wide; striae 12–13 in 10 μm. It was scattered from 360 to 180 cm. At 360 cm maximum relative density of 6.7 percent was observed.

***Pinnularia*** **species 2:** Valve 40 μm long by 10 μm wide; striae 12 in 10 μm; isolated punctum in central area. A few frustules were observed at 270 cm.

## CYMBELLACEAE

***Cymbella amphicephala*** **Naeg. *ex* Kützing:** Valve 30–32 μm long by 8–10 μm wide; striae 14–16 in 10 μm (Patrick and Reimer 1975:33). Frustules were observed only in deeper strata (from 360 cm to 195 cm). A maximum frequency of 1.7 percent was observed from 360 cm.

***Cymbella angustata*** **(W. Sm.) Cleve:** Valve 35–43 μm long by 8–9 μm wide; striae 16–20 in 10 μm (Patrick and Reimer 1975:22). It was observed from 345 cm to 210 cm. A few frustules were also observed from 165 cm and 30 cm. A maximum relative density of 3.1 percent was observed from 315 cm.

***Cymbella cuspidata*** **Kützing:** Valve 80–90 μm long by 22 μm wide; striae 13–14 in 10 μm (Patrick and Reimer 1975:39). Frustules were observed only at 285 and 270 cm. Their relative density was 0.5 percent.

***Cymbella hebridica*** **Grun. *ex* Cleve:** Valve 28–35 μm long by 7–8 μm wide; striae 11–16 in 10 μm (Patrick and Reimer 1975:30). It was observed from 330 to 15 cm and in extant samples. A maximum relative density of 14 percent was observed from 165 cm.

***Cymbella heteropleura*** **var. *subrostrata*** **Cleve:** Valve 175–177 μm long by 45–47 μm wide; striae 11–12 in 10 μm (Patrick and Reimer 1975:38). It was observed from 315 to 255 cm and at 195 cm. A maximum relative density of 0.5 percent was observed from 285 cm.

***Cymbella lunata*** **W. Smith:** Valve 35–55 μm long by 5–8 μm wide; striae 10–14 in 10 μm (Patrick and Reimer 1975:46). Frustules were scattered from 360 to 60 cm and were also observed in extant samples. A maximum relative density of 10.2 percent was observed from 345 cm.

***Cymbella minuta*** **Hilse *ex* Rabenhorst:** Valve 18–19 μm long by 5–7 μm wide; striae 12–14, becoming 18–19 in 10 μm (Patrick and Reimer 1975:47). It was observed from 360 to 255 cm. A maximum relative density of 9.1 percent was observed from 360 cm.

***Cymbella minuta*** **f. *latens*** **(Krasske) Reimer:** Valve 23–24 μm long by 6–7 μm wide; striae 12 in 10 μm (Patrick and Reimer 1975:49). It was scattered from 330 to 105 cm and was also observed in extant samples.

The maximum relative density of 2.4 percent was observed from 180 cm.

***Cymbella naviculiformis*** **Auersw. *ex* Heib.:** Valve 40–42 μm long by 10–11 μm wide; striae 13–14 in 10 μm (Patrick and Reimer 1975:31). It was observed from 330 and 315 cm, 180 cm, and from 135 to 75 cm. The maximum relative density of 6 percent was observed from 330 cm and 135 cm.

***Cymbella perpusilla*** **A. Cleve:** Valve 16 μm long by 4 μm wide; striae to 16 in 10 μm (Hustedt 1930:361). Frustules were observed only from 300 cm to 225 cm and from 150 cm. The maximum relative density of 6.2 percent was observed from 150 cm.

***Cymbella sinuata*** **Gregory:** Valve measurements not recorded (Patrick and Reimer 1975:51). One specimen was observed from 195 cm.

***Cymbella turgida*** **(Greg.) Cleve:** Valve 52 μm long by 12 μm wide; striae 10 in 10 μm (Hustedt 1930:358). One frustule was observed from 315 cm.

***Amphora ovalis*** **(Kütz.) Kützing:** Valve 33–40 μm long by 10–12 μm wide; striae 12 in 10 μm (Patrick and Reimer 1975:68). One frustule was observed at each of four levels and also in the extant plankton.

## GOMPHONEMACEAE

***Gomphonema acuminatum*** **Ehrenberg:** Valve 35–40 μm long by 7–8 μm wide; striae 12 in 10 μm (Patrick and Reimer 1975:112). One frustule was observed at 270 cm.

***Gomphonema affine*** **Kützing:** Valve 30 μm long by 7 μm wide; striae 14 in 10 μm (Patrick and Reimer 1975:133). Only one or two frustules were observed at 240 cm.

***Gomphonema angustatum*** **var. *intermedia*** **Grunow:** Valve 27 μm long by 8 μm wide; striae 12 in 10 μm (Patrick and Reimer 1975:126). One specimen was observed from 135 cm.

***Gomphonema apicatum*** **Ehrenberg:** Valve 35–36 μm long by 8 μm wide; striae 12–13 in 10 μm (Patrick and Reimer 1975:110). Frustules were observed only from 210 cm and 180 cm where their relative density was 0.4 percent and 0.2 percent respectively.

***Gomphonema gracile*** **Ehrenberg em. V. H.:** Valve 40–42 μm long by 6.5–7 μm wide; striae 16 in 10 μm (Patrick and Reimer 1975:131). Frustules were scattered from 345 cm to 165 cm. A maximum relative density of 0.7 percent was observed from 285 cm.

***Gomphonema grunowii*** **Patrick:** Valve 38 μm long by 7 μm wide; striae 12 in 10 μm (Patrick and Reimer 1975:131). It was observed from 330 cm, 300 to 285 cm, and 210 cm. A maximum relative density of 0.5 percent was observed from 330 cm.

***Gomphonema olivaceum*** **(Lyngb.) Kützing:** Valve 23–25 μm long by 6.5–7 μm wide; striae 12 in 10 μm (Patrick and Reimer 1975:139). Frustules were observed from 360 cm, 315 cm, and 180 to 135 cm. The maximum relative density of 6.4 percent was observed from 150 cm.

***Gomphonema parvulum*** **(Kützing):** Valve 29 μm long by 6 μm wide; striae 12 in 10 μm (Patrick and Reimer 1975:122). Only one or two frustules were observed at 270 cm.

***Gomphonema subtile*** **Ehrenberg:** Valve 43–45 μm long by 5 μm wide; striae 16 in 10 μm (Patrick and Reimer 1975:117). A few specimens were observed from 270 cm.

***Gomphonema truncatum*** **var. *capitatum*** **(Ehr.) Patrick:** Valve 25–50 μm long by 10–15 μm wide; striae about 13 in 10 μm (Patrick and Reimer 1975:119). Frustules were scattered between 330 and 195 cm and were also found from 135 cm. The maximum relative density of 1.2 percent was observed from 195 cm. One frustule was in the extant plankton.

## EPITHEMIACEAE

***Denticula elegans*** **f. *valida*** **Pedicino:** Valve 35–55 μm long by 5–10 μm wide; costae 3–4 in 10 μm; striae 5–6 between costae (Patrick and Reimer 1975:171). One or two frustules were observed from 180, 150, and 120 cm.

***Rhopalodia gibba*** **(Ehr.) O. Müller:** Valve 120–155 μm long by 7–8.5 μm wide; costae 7 in 10 μm; striae 1–2 between costae (Patrick and Reimer 1975:189). One frustule was observed from 135 cm and three were observed from 105 cm and 90 cm.

***Rhopalodia gibberula*** **var. *protracta*** **Grunow:** Valve 40–60 μm long by 8–11 μm wide; costae 3–4 in 10 μm; striae 14–16 in 10 μm (Hustedt 1930:391). It was rare from 150, 135, 90, and 75 cm.

***Epithemia sorex* Kützing:** Valve 35–37 μm long by 9–9.5 μm wide; costae 5 in 10 μm; 3–4 rows of alveoli between costae (Patrick and Reimer 1975:188). It was observed from 135 cm and 105 to 75 cm. At 105 cm the maximum relative density of 1 percent was observed.

***Epithemia turgida* (Ehr.) Kützing:** Valve 140–145 μm long by 18–20 μm wide; costae 4 in 10 μm; two rows of alveoli between costae (Patrick and Reimer 1975:182). Frustules were observed from 150 to 75 cm. A maximum relative density of 1.2 percent was observed from 120 cm.

***Epithemia turgida* var. *westermannii* (Ehr.) Grunow:** Valve 70–72 μm long by 14 μm wide; costae 4 in 10 μm; two rows of alveoli between costae (Patrick and Reimer 1975:184). One frustule was observed from 165 cm.

### NITZSCHIACEAE

***Nitzschia dissipata* (Kütz.) Grunow:** Valve 24 μm long by 3–4 μm wide; keel punctae 8–10 in 10 μm; striae very fine (Hustedt 1930:412). A few frustules were observed at 120 cm.

***Nitzschia fonticola* Grunow:** Valve 9–16 μm long by 3–3.5 μm wide; keel punctae 12–14 in 10 μm; striae very fine (Hustedt 1930:415). Frustules were observed from 345 to 210 cm. A few frustules were scattered at 165, 90, and 30 cm. The maximum relative density of 6 percent was observed from 285 cm.

***Nitzschia frustulum* (Kütz.) Grunow:** Valve 20–22 μm long by 3–4 μm wide; keel punctae 11–12 in 10 μm; striae 20 in 10 μm (Hustedt 1930:415). It was only in deeper strata from 360 to 225 cm. The maximum relative density of 7.3 percent was obtained from 240 cm.

***Nitzschia palea* (Kütz.) W. Smith:** Valve 30–32 μm long by 2.5–3 μm wide; keel punctae 12 in 10 μm; striae very fine (Hustedt 1930:416). Frustules were scattered from 345 to 90 cm, at 15 cm and in extant samples. The maximum relative density of 5.2 percent was observed from 180 and 15 cm.

***Nitzschia* species:** Valve linear-lanceolate, 65–67 μm long by 7–7.5 μm wide; keel punctae 8 in 10 μm; striae 20 in 10 μm. Specific identification of this taxon was not possible. It resembles *N. thermalis* in general shape but differs in shape of the poles. It also resembles *N. capitellata* in general shape but the number of striae is different. It resembles *N. angustata* in shape but the striae in *N. angustata* are much coarser. One frustule was found from 360 cm, 5 from 150 cm, and 8 from 135 cm.

***Hantzschia amphioxys* f. *capitata* O. Müller:** Valve 30–52 μm long by 7–10 μm wide; keel punctae 8–10 in 10 μm; striae about 20 in 10 μm (Hustedt 1930:394). Frustules were observed from 225 to 60 cm. At 135 cm they constituted 16.2 percent of the diatom population.

### SURIRELLACEAE

***Cymatopleura solea* (Bréb.) W. Smith:** Valve 65–70 μm long by 10–15 μm wide; costae 4–6 in 10 μm; striae not clearly observed (Hustedt 1930:425). Frustules were observed at 285 cm.

***Surirella ovalis* Brébisson:** Valve measurements not recorded (Hustedt 1930:441). One frustule was observed at 120 cm.

***Surirella robusta* Ehrenberg:** Valve 120–145 μm long by 40–65 μm wide; costae 1–2 in 10 μm; striae 8–12 in 10 μm (Hustedt 1930:437). A few frustules were observed at 360 cm.

## Distribution and Abundance

The occurrence and abundance of diatoms in 27 samples taken from the core were determined. The highest counts were for nonplanktonic species, belonging mainly to the genera *Cymbella*, *Pinnularia*, *Navicula*, *Gomphonema*, and *Eunotia*. Planktonic forms encountered belonged mainly to the genera *Cyclotella*, *Melosira*, *Fragilaria*, *Stephanodiscus* and *Tabellaria*.

The abundance of all taxa whose frequency was four or more in any sample is shown in Figure 2. This figure is prepared with planktonic taxa on the right and periphytic taxa on the left. The three most abundant species by far in this study were *Navicula subtilissima*, *Pinnularia microstauron*, and *Tabellaria fenestrata*. *Anomoeoneis serians* var. *brachysira*, *Cymbella hebridica*, *Cymbella lunata*, *Fragi-*

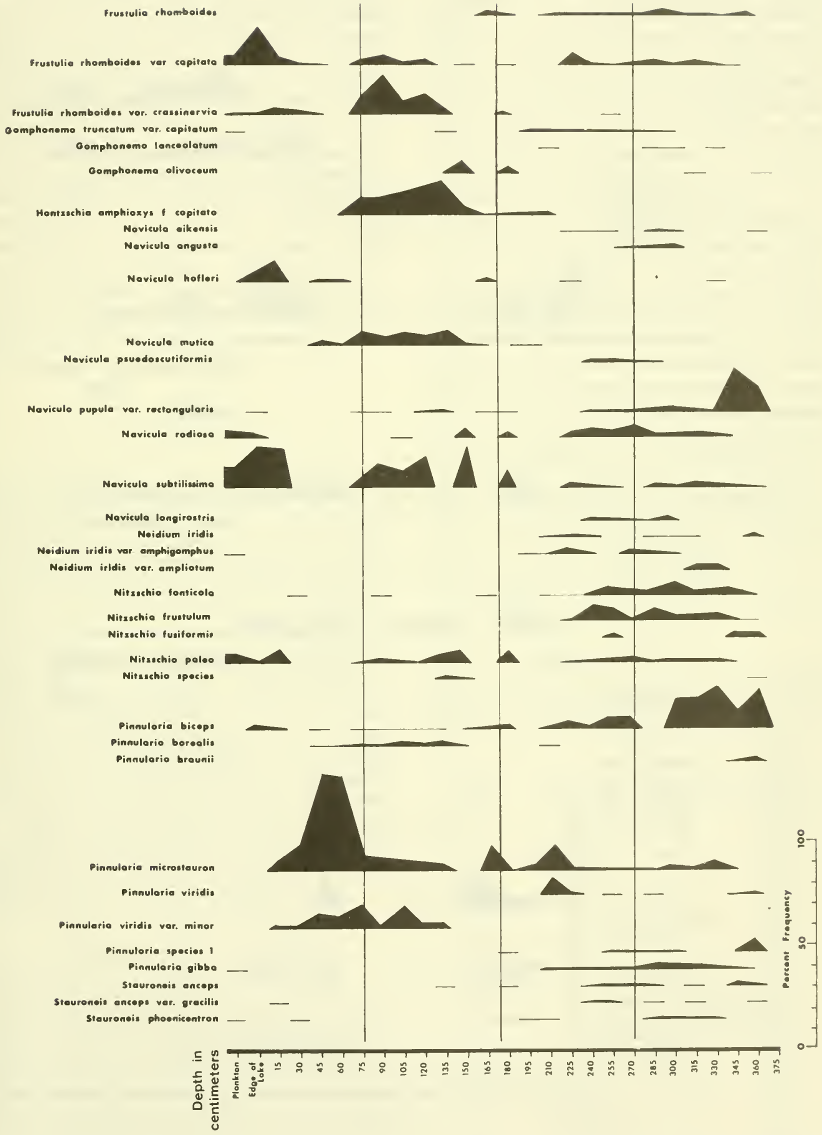

Fig. 2. Percent frequency of individual diatom taxa according to sediment depth. Euplankters are listed at the top of the figure. Scale of frequency width is shown on the bottom right.

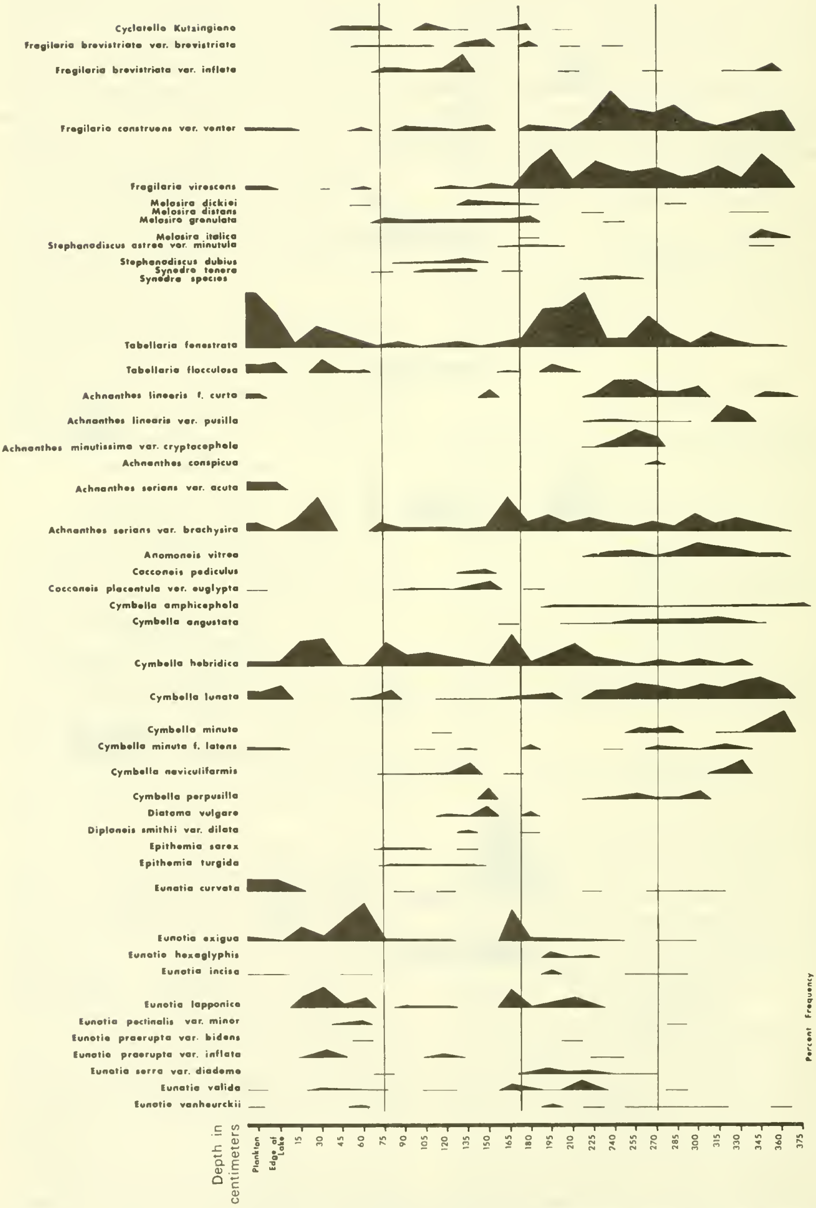

Fig. 2 continued.

*laria construens* var. *venter, Fragilaria viriscens, Frustulia rhomboides* var. *capitata, Pinnularia biceps,* and *Tabellaria fenestrata* were also common, though their populations fluctuated greatly in samples at different depths. Species of *Eunotia* were important from 210 to 120 cm and from 60 to 15 cm. *Fragilaria construens* var. *venter* and *Fragilaria virescens* were predominent from 360 to 165 cm and then dropped out suddenly. *Frustulia rhomboides* var. *crassinervia, Hantzchia amphioxys* f. *capitata, Navicula mutica, N. subtillissima,* and *Pinnularia viridis* var. *minor* showed sudden peaks between 150 and 75 cm. *Navicula pupula* var. *rectangularis* appeared in great numbers from 360 cm to 330 cm, and *Pinnularia microstauron* was prevalent from 60 cm to 30 cm.

### Species Diversity

The number of taxa occurring at each sample depth was plotted against depth (Table 1) to provide a graphic representation of floristic changes through time (Fig. 3). The number of taxa encountered per sample varied but was maximum at 285 cm and minimum at 30 cm. In the deeper samples (360 to 285 cm) the number of taxa observed was elevated and a more or less continuous decrease to the present was evident. Some deviation from this trend could be observed from the 180 to 135 cm depths.

Species diversity values for the diatom population are given in Table 1. Species diversity was plotted against depth to provide a graphic representation of diversity change through time (Fig. 4). Diversity values were higher in deeper (earlier) samples than in the shallower (more recent) samples.

### Cluster Analysis of Samples

The results of the cluster analysis of samples are presented in a dendogram (Fig. 5), with the similarity between any two samples expressed as the height of horizontal lines joining them. The degrees of similarity are given as percentages (similarity coefficient of Ruzicka, 1958) on the left hand scale. Table 2 lists species important in the formation of clusters.

Our analysis of 26 samples clustered into two major groups (Fig. 5), one composed primarily of the deeper sediment samples (Group I = sample 2 through 14 with the exception of sample 12 and two modern samples) and the other of more recent samples. The former is internally more similar and clusters above the 20 percent similarity level, and the latter clustered at the 13.5 percent level. Each of these major groups is in turn composed of two subgroups (Fig. 5).

Subgroup A is a time (= depth) discreet unit of the deepest sediments (samples 2–10). The diatoms which characterize and are dominant in this subgroup include *Pinnularia biceps, Fragilaria construens* var. *venter, Nitzschia frustulum, Navicula pupula* var. *rectangularis, Nitzschia fonticola, Anomoeoneis vitrea,* and *Achnanthes linearis* f. *curta.* When the ecological preferences of these and other species common here are examined, an interesting pattern emerges. The aquatic environment through the depositional period of this subgroup must have been no more acid than circumneutral or, more likely, rather alkaline. The lake likewise appears to have been oligotrophic to mesotrophic.

Subgroup B does not represent a discreet

TABLE 1. Number of diatom species encountered and Shannon-Weaver species diversity index for each sample studied.

| Sample Number | Depth of Sample (cm) | No. of Species in Sample | Species Diversity Index |
|---|---|---|---|
| 2 | 360 | 35 | 2.78 |
| 3 | 345 | 36 | 2.71 |
| 4 | 330 | 33 | 2.91 |
| 5 | 315 | 40 | 3.13 |
| 6 | 300 | 36 | 3.10 |
| 7 | 285 | 53 | 3.31 |
| 8 | 270 | 50 | 3.24 |
| 9 | 255 | 47 | 3.23 |
| 10 | 240 | 44 | 3.12 |
| 11 | 225 | 45 | 2.89 |
| 12 | 210 | 38 | 2.39 |
| 13 | 195 | 27 | 2.22 |
| 14 | 180 | 43 | 2.75 |
| 15 | 165 | 28 | 2.16 |
| 16 | 150 | 30 | 2.41 |
| 17 | 135 | 42 | 2.68 |
| 18 | 120 | 36 | 2.60 |
| 19 | 105 | 35 | 2.53 |
| 20 | 90 | 30 | 2.31 |
| 21 | 75 | 28 | 2.38 |
| 22 | 60 | 24 | 1.64 |
| 23 | 45 | 19 | 1.51 |
| 24 | 30 | 17 | 2.19 |
| 25 | 15 | 20 | 2.25 |
| 26 | Surface | 19 | |

time unit of sediments. It is composed essentially of midcore samples admixed with our two modern samples. The diatoms which characterize this subgroup include *Tabellaria fenestrata, Frustulia rhomboides* var. *capitata, Eunotia curvata, Anomoeoneis serians* var. *acuta* and, *Eunotia serra* var. *diadema.* These organisms and others present in this subgroup indicate that the environment in the lake changed from oligo-mesotrophic and alkaline toward dystrophy during the time of deposition of sediments around the 210–225 cm level from the present lake surface. However, this must have also been a time of some environmental disturbance due to the rather low level of clustering in subgroup B and due to the mixed nature of the subgroup.

Subgroup C is a time discreet unit from the more recent sediments. It is characterized by *Navicula mutica, Frustulia rhomboides, Hantzschia amphioxys* f. *capitata, Fragilaria brevistriata* var. *inflata,* and *Pinnularia borealis.* These organisms, together with others common here, indicate circumneutral to somewhat acidic conditions. The lake apparently was less dystrophic than during the short depositional interval above the 225 cm level. Such conditions prevailed for a reasonably long depositional period (at least 150 cm).

Subsequently a new depositional environment evolved which was most similar to that of deposition of subgroup B. Thus, subgroup D is characterized by many species which

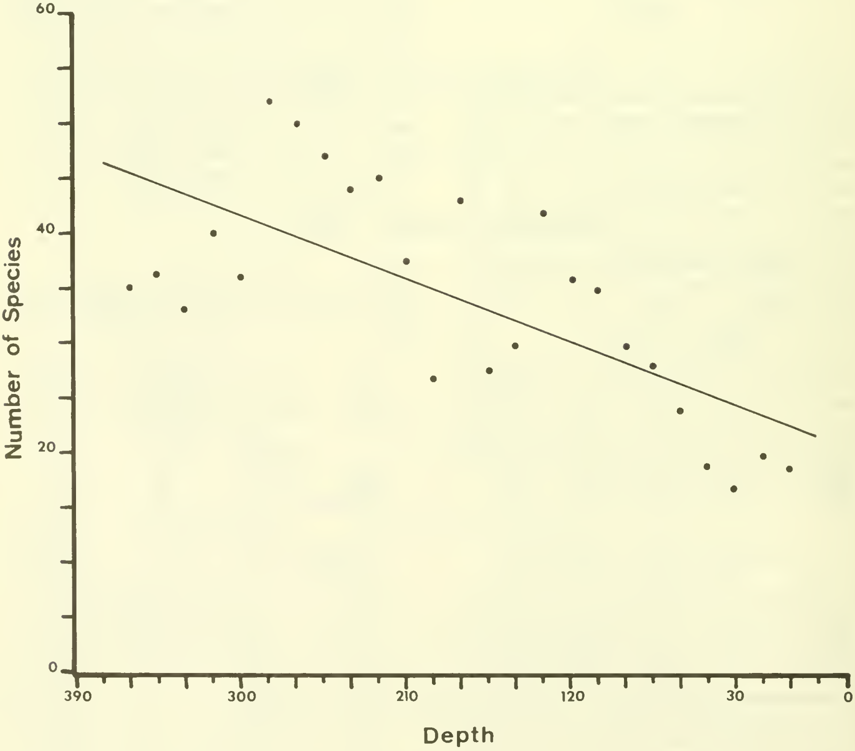

Fig. 3. Number of diatom species in relation to sediment depth. r = 0.602, which is significant at the 0.01 level.

prefer cool acidic (dystrophic) conditions. Delineating species of this subgroup include *Eunotia exigua*, *Eunotia lapponica*, *Eunotia valida*, *Pinnularia microstauron*, and *Pinnularia viridis*.

From this information, it seems clear that four major depositional periods occurred in Lily Lake. The first was characterized by somewhat alkaline oligotrophic to mesotrophic conditions and lasted through about 135 cm of deposition. The second can be characterized by increasingly acidic waters, and lasted through a period of deposition from roughly 225 cm to 150 cm. However, this pe-

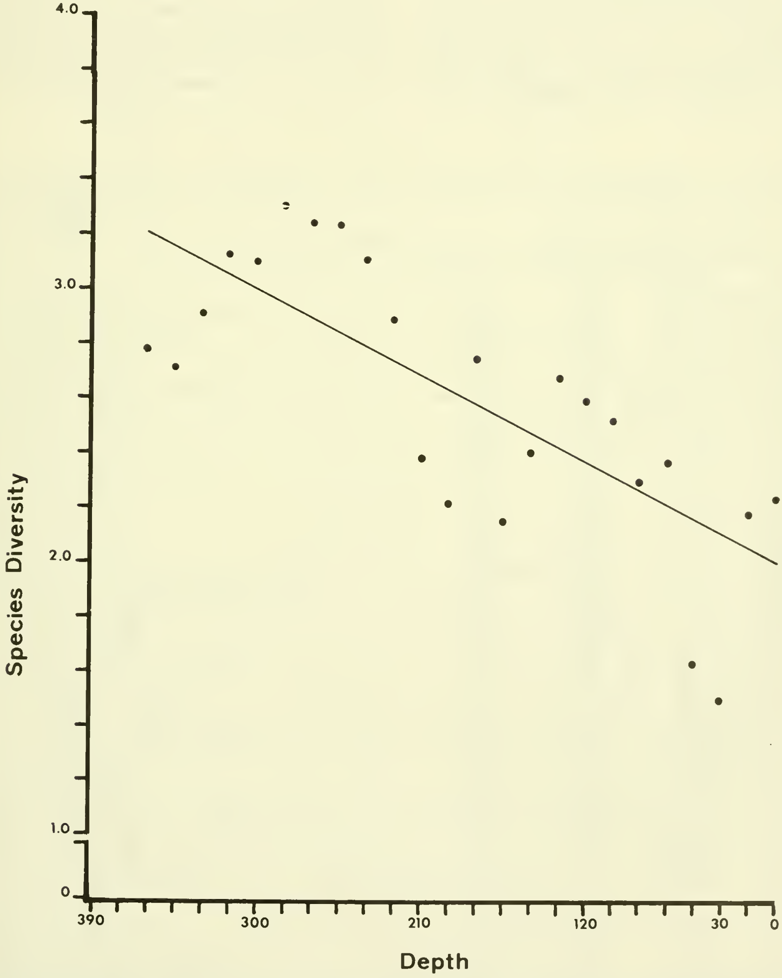

Fig. 4. Shannon-Weaver diversity indices for diatom populations in relation to sediment depth. r = 0.754, which is significant at the 0.01 level.

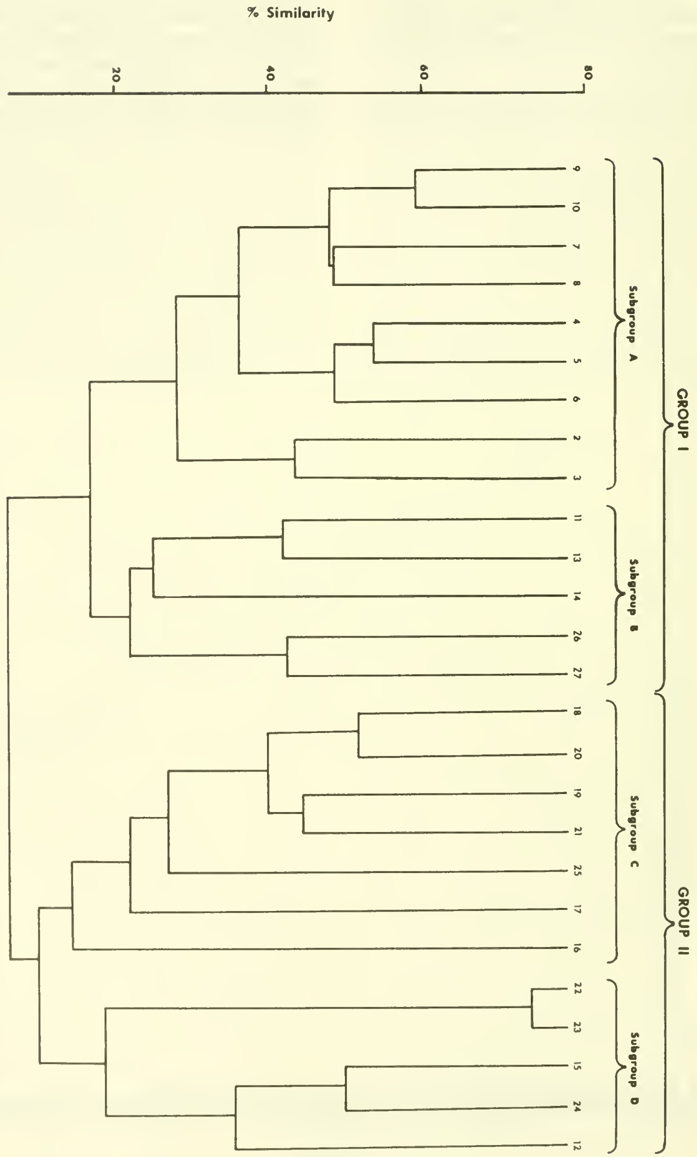

Fig. 5. Phenogram (cluster diagram) demonstrating similarity between samples from different sediment depths. Sample numbers are shown within subgroups and correspond to depth, with sample 2 being the deepest (oldest) and samples 26 and 27 being surface samples.

riod was not as homogenous as the others, and depositional environments apparently fluctuated and eventually disrupted the development of acidic conditions. This disturbance interrupted the development of strictly dytrophic conditions and apparently shifted the system toward a new period of circumneutral mesotrophic (?) conditions. Recent conditions in the lake were again less stable but appear to be returning to a more acidic, dystrophic state. This could explain why our surface samples clustered with those of deeper sediments (in subgroup B).

## Prevalent Species and Cluster Analysis

A list of species encountered in this study and identified as prevalents is given in Table 3. Prevalent species were selected based upon their occurrence in 30 percent or more of the samples. These species were subjected to niche breadth and niche overlap analyses (Colwell and Fatuyma 1971; Table 3). Species were then clustered based upon niche overlap values (Cody 1974). This analysis represents an attempt to group diatom species according to preference for similar environmental and/or habitat conditions. Three

**Table 2.** Clusters (subgroups) as delineated on Figure 5. The prominent species responsible for the uniqueness of subgroups are shown.

| Species | Cluster subgroups (Fig. 5) | | | |
|---|---|---|---|---|
| | A | B | C | D |
| *Pinnularia biceps* | 11.17 | 1.58 | 0.57 | 0.32 |
| *Fragilaria construens* var. *venter* | 8.81 | 2.08 | 0.86 | 0.10 |
| *Achnanthes linearis* f. *curta* | 3.21 | 0.68 | 0.60 | 0.0 |
| *Anomoeoneis vitrea* | 2.97 | 0.10 | 0.0 | 0.0 |
| *Cymbella lunata* | 6.76 | 4.12 | 0.20 | 0.04 |
| *Navicula pupula* var. *rectangularis* | 3.88 | 0.24 | 0.34 | 0.04 |
| *Cymbella minuta* | 2.21 | 0.0 | 0.0 | 0.0 |
| *Nitzschia fonticola* | 3.37 | 0.14 | 0.11 | 0.24 |
| *Fragilaria virescens* | 8.88 | 8.74 | 0.66 | 1.36 |
| *Achnanthes linearis* var. *pusilla* | 2.12 | 0.22 | 0.0 | 0.0 |
| *Pinnularia* species 1 | 1.19 | 0.08 | 0.0 | 0.0 |
| *Navicula radiosa* | 3.51 | 2.18 | 0.83 | 0.0 |
| *Nitzschia frustulum* | 3.67 | 0.18 | 0.0 | 0.0 |
| *Cymbella angustata* | 1.42 | 0.04 | 0.0 | 0.16 |
| *Pinnularia* species 2 | 1.60 | 0.26 | 0.0 | 0.12 |
| *Achnanthes minutissima* var. *cryptocephala* | 1.98 | 0.14 | 0.0 | 0.0 |
| *Neidium iridis* var. *amphigomphus* | 1.24 | 0.18 | 0.03 | 0.08 |
| *Tabellaria fenestrata* | 4.66 | 17.86 | 1.51 | 8.48 |
| *Navicula subtilissima* | 1.02 | 8.20 | 10.97 | 0.0 |
| *Frustulia rhomboides* var. *capitata* | 0.89 | 4.66 | 2.34 | 0.40 |
| *Eunotia curvata* | 0.09 | 2.46 | 0.31 | 0.0 |
| *Anomoeoneis serians* var. *acuta* | 0.0 | 1.76 | 0.0 | 0.0 |
| *Eunotia serra* var. *didyma* | 0.22 | 1.22 | 0.03 | 0.36 |
| *Anomoeoneis serians* var. *brachysira* | 4.43 | 4.96 | 2.80 | 7.48 |
| *Pinnularia microstauron* | 1.28 | 0.90 | 4.54 | 25.84 |
| *Cymbella hebredica* | 1.73 | 3.42 | 5.77 | 7.76 |
| *Eunotia lapponica* | 0.0 | 1.20 | 1.14 | 6.28 |
| *Tabellaria flocculosa* | 0.0 | 2.48 | 0.0 | 1.76 |
| *Eunotia valida* | 0.06 | 0.60 | 0.23 | 2.56 |
| *Eunotia exigua* | 0.13 | 1.02 | 1.60 | 9.80 |
| *Pinnularia viridis* | 0.30 | 0.04 | 0.0 | 1.48 |
| *Pinnularia viridis* var. *minor* | 0.0 | 0.0 | 5.49 | 3.48 |
| *Navicula mutica* | 0.02 | 0.20 | 3.46 | 0.40 |
| *Frustulia rhomboides* | 0.02 | 0.56 | 7.63 | 0.80 |
| *Nitzschia palea* | 1.30 | 2.14 | 2.37 | 0.0 |
| *Hantzschia amphioxys* f. *capitata* | 0.0 | 0.36 | 7.29 | 0.44 |
| *Pinnularia borealis* | 0.0 | 0.0 | 1.29 | 0.44 |
| *Fragilaria brevistriata* var. *inflata* | 0.0 | 0.20 | 2.8 | 0.0 |

*Figures are mean importance values as determined by multiplying presence times average relative frequency (Warner and Harper 1972).

major clusters are evident from this analysis.

Most species in the first cluster (group I, Fig. 6) flourished during the earliest period of sedimentation (from sample 2 at 360 cm to sample 12 at 210 cm). The majority of species in the cluster for which ecological preferences are known are generally considered to be pH indifferent or alkaliphilous, saproxenous to mesosaprobic and to prefer oligotrophic to eutrophic conditions. The species in this cluster correspond well with the species prominent in subgroup A (Table 2) of the sample cluster (Fig. 5). This is further evidence for the nondystrophic nature of Lily Lake early in its depositional history.

The species in group II (Fig. 6) correspond well with the species which delineate subgroup C of Figure 5. As previously noted, subgroup C represents a time discreet unit of deposition which followed a short period of dystrophy and disturbance. The species for which ecological preferences are known in group II (Fig. 6) are indifferent to pH or prefer alkaline waters, are oligosaprobic to mesosaprobic, and occur in mesotrophic to eutrophic waters. These results show more strongly than sample clustering the fact of a second oligo-mesotrophic period in the lake history. This period corresponds approximately with deposition levels from 150 cm to 60 cm.

Group III (Fig. 6) includes species from both subgroups B and D of Table 2 and Figure 5. The species of group III with known ecological preferences are indicative of acidic waters and often dystrophic or bog habitats. This group is composed of species found in midcore and surface sediments. The fact that these species overlap in their niche preferences even though widely separated depositionally gives additional strength to our hypothesis of a period of dystrophy following the first oligo-mesotrophic period in the lake history which was disrupted and followed by a second oligo-mesotrophic period. The lake has apparently returned recently to an acidic dystrophic condition that is very similar to the earlier dystrophic period.

Also of interest are the species association patterns displayed in the phenogram in Figure 6. Based on the patterns of species associations determined by niche overlap, it is possible to infer physico-chemical requirements

TABLE 3. List of 45 species occurring in 30 percent or more of the samples. Relative niche breadth and niche overlap values are reported for all species.

| Species Name | Relative Niche Breadth | Average Niche Overlap |
|---|---|---|
| *Achnanthes linearis* var. *pusilla* | 53.701 | 31.245 |
| *Achnanthes linearis* f. *curta* | 68.383 | 30.171 |
| *Anomoeoneis serians* var. *brachysira* | 89.400 | 49.244 |
| *Anomoeoneis vitrea* | 66.324 | 38.018 |
| *Cyclotella kützingiana* | 71.928 | 28.309 |
| *Cymbella amphicephala* | 70.015 | 37.349 |
| *Cymbella angustata* | 66.395 | 38.523 |
| *Cymbella hebridica* | 86.469 | 44.138 |
| *Cymbella lunata* | 83.010 | 47.525 |
| *Cymbella minuta* f. *latens* | 72.314 | 39.631 |
| *Cymbella naviculiformis* | 55.657 | 28.322 |
| *Eunotia curvata* | 55.833 | 22.718 |
| *Eunotia exigua* | 73.128 | 28.090 |
| *Eunotia incisa* | 69.010 | 33.792 |
| *Eunotia lapponica* | 74.453 | 29.151 |
| *Eunotia praerupta* var. *inflata* | 58.251 | 23.606 |
| *Eunotia valida* | 73.148 | 30.748 |
| *Eunotia vanheurcki* | 71.241 | 30.136 |
| *Fragillaria brevistriata* | 68.657 | 29.118 |
| *Fragillaria brevistriata* var. *inflata* | 64.588 | 19.859 |
| *Fragilaria construens* var. *venter* | 78.679 | 45.792 |
| *Fragilaria virescens* | 82.047 | 46.837 |
| *Frustulia rhomboides* | 73.972 | 40.406 |
| *Frustulia rhomboides* var. *capitata* | 73.770 | 36.534 |
| *Frustulia rhomboides* var. *crassinervia* | 67.992 | 28.289 |
| *Gomphonema truncatum* var. *capitatum* | 69.813 | 38.090 |
| *Hantzschia amphioxys* f. *capitata* | 64.866 | 28.329 |
| *Melosira granulata* | 67.492 | 29.150 |
| *Navicula heufleri* | 58.306 | 20.246 |
| *Navicula mutica* | 67.445 | 29.306 |
| *Navicula pupula* var. *rectangularis* | 62.431 | 33.632 |
| *Navicula radiosa* | 81.112 | 44.717 |
| *Navicula subtilissima* | 75.065 | 33.805 |
| *Neidium iridis* var. *amphigomphus* | 63.813 | 35.999 |
| *Nitzschia fonticola* | 71.934 | 41.987 |
| *Nitzschia frustulum* | 65.923 | 38.151 |
| *Nitzschia palea* | 81.747 | 43.753 |
| *Pinnularia biceps* | 75.766 | 44.059 |
| *Pinnularia borealis* | 68.856 | 29.436 |
| *Pinnularia microstauron* | 70.695 | 32.405 |
| *Pinnularia viridis* var. *minor* | 70.814 | 29.710 |
| *Pinnularia gibba* | 70.770 | 41.579 |
| *Pinnularia brebissonii* | 63.346 | 33.225 |
| *Tabellaria fenestrata* | 87.658 | 46.379 |
| *Tabellaria flocculosa* | 66.297 | 24.348 |

of some diatom taxa which are not well discussed in the literature. For example, *Anomoeoneis vitrea* and *Nitzschia frustulum* var. *perminuta* cluster at .94 niche overlap. Such a high overlap value (on a scale of 0.0–1.0) indicates that their niches are highly similar. This should indicate that these two diatoms have similar ecological requirements. The same type of information can be obtained for several other species pairs as illustrated in Figure 6.

## pH and Saprobien Spectra

The percent sum frequency of alkaliphilous, pH indifferent, and acidophilous taxa present at each level of deposition was calculated. Taxa used in this analysis are list-

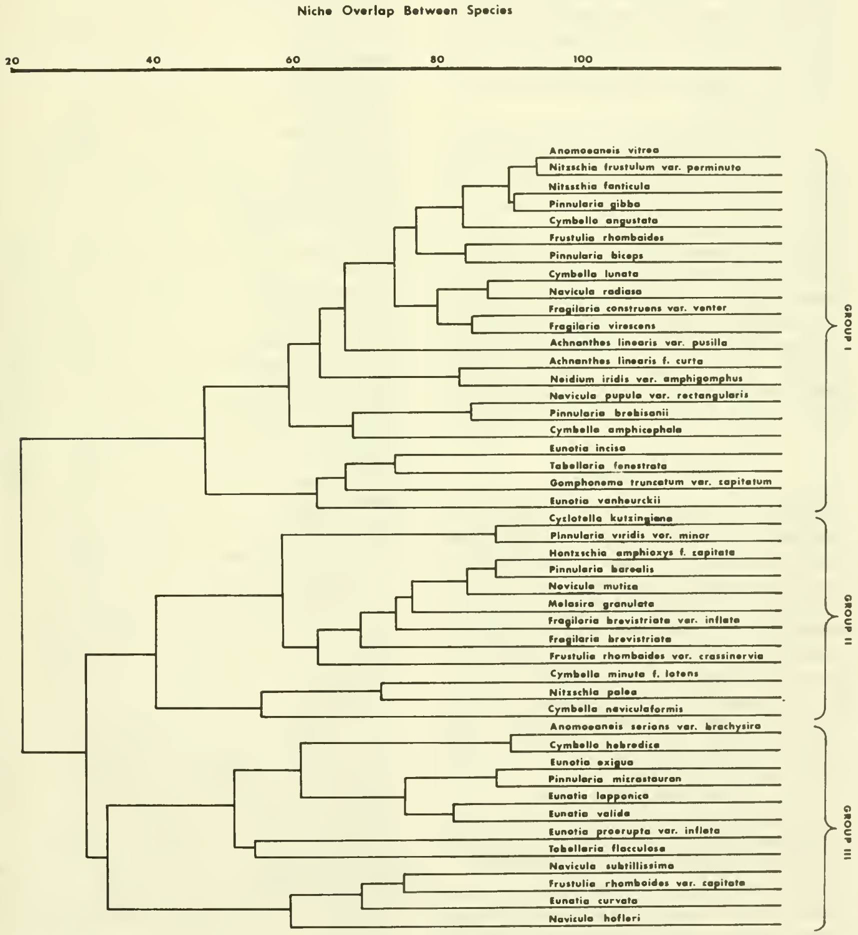

Fig. 6. Phenogram (cluster diagram) demonstrating similarity in occupied niche by comparing average niche overlap.

ed in Table 4. The percent sum frequency of these taxa was plotted against depth to provide a graphic representation of pH preference changes of the diatom populations through time (Fig. 7). Alkaliphilous species show essentially two highs. The first is in the earliest sediments and the second occurs approximately from 180 cm to 60 cm (Fig. 7). Acidophilous species increased through the early history of the lake, eventually displacing the alkaliphilous forms. However, acidophilous species decreased drastically betwen 180 and 150 cm and continued in relatively low levels until about 60 cm, where they again became prominent and remained so to the surface.

Similarly a graph of percent sum frequency of the taxa indicative of different saprobien conditions was plotted against depth (Table 4; Fig. 8). It appears from the graph that the number of mesosaprobic species has gradually increased through time while the number of oligosaprobic and saproxenous species has decreased. This provides general evidence for an early oligo-mesotrophic system that has become increasingly dystrophic through time. The two cycles previously suggested for the system with a period of disturbance can also be inferred from Figure 8.

## General Discussion

Pleistocene glaciation of the Uinta Mountains has not been thoroughly investigated (but see Atwood 1905, Hansen 1969). Therefore chronological information on distinct Pleistocene glacial advances is not available. However, Richmond (1965) has given an excellent chronological account of Pleistocene glaciation of the Rocky Mountains. According to his observations Pleistocene glaciation consisted of Pre-Bull Lake glaciation, Bull Lake glaciation, Pinedale glaciation, and Neoglaciation. Various $C^{14}$ dates recorded from the Rocky Mountain region on Bull Lake glacial deposits range from 42,000 to 25,000 years B.P.; those of Pinedale deposits range from 25,000 to 11,300 years B.P. Deposits of two minor glacial advances have formed in the cirques of the Rocky Mountains since the end of the altithermal interval, which together represent the Neoglaciation. Alluviation during the Temple Lake Stade

TABLE 4. List of species encountered in this study with known pH and/or spaprobien condition preferences. Columns designate physiological response syndromes (see the footnote at the end of the table).

| | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| *Achnanthes linearis* f. *curta* | | X | | X | | |
| *Amphora ovalis* | X | | | | X | |
| *Anomoeoneis vitrea* | | X | | X | | |
| *Cocconeis placentula* var. *euglypta* | X | | | | X | |
| *Cyclotella kutzingiana* | | X | | | | X |
| *Cyclotella meneghiniana* | X | | | | | X |
| *Cymbella naviculiformis* | | X | | | X | |
| *Cymbella sinuata* | | X | | | | |
| *Cymbella turgida* | X | | | | X | |
| *Denticula elegans* | X | | | | | |
| *Diatoma vulgare* | X | | | | | X |
| *Diploneis elliptica* | | X | | X | | |
| *Diploneis interrupta* | X | | | | | |
| *Epithemia sorex* | X | | | X | | |
| *Epithemia turgida* | X | | | X | | |
| *Eunotia curvata* | | | X | | X | |
| *Eunotia pectinalis* | | | | | | |
| *Eunotia pectinalis* var. *minor* | | X | | | X | |
| *Fragilaria brevistriata* | X | | | | X | |
| *Fragilaria brevistriata* var. *inflata* | X | | | | | |
| *Fragilaria construens* var. *venter* | X | | | | | X |
| *Fragilaria crotonensis* | X | | | | X | |
| *Fragilaria leptostauron* | X | | | | X | |
| *Fragilaria virescens* | | X | | | X | |
| *Frustulia rhomboides* | | | X | X | | |
| *Gomphonema angustatum* | X | | | | X | |
| *Gomphonema gracile* | | X | | | | |
| *Gomphonema olivaceum* | X | | | | X | |
| *Gomphonema truncatum* var. *capitatum* | X | | | | X | |
| *Hantzschia amphioxys* f. *capitata* | X | | | | | X |
| *Melosira distans* | | | X | X | | |
| *Melosira granulata* | X | | | | X | |
| *Melosira italica* | X | | | | X | |
| *Navicula mutica* | X | | | | | |
| *Navicula pseudoscutiformis* | | X | | X | | |
| *Navicula pupula* var. *rectangularis* | | X | | | | |
| *Navicula radiosa* | | X | | | X | |
| *Neidium bisulcatum* | | X | | | | X |
| *Neidium iridis* | | X | | | X | |
| *Nitzschia fonticola* | X | | | | | X |
| *Nitzschia palea* | | X | | | | X |
| *Pinnularia borealis* | | X | | | X | |
| *Pinnularia gibba* | | | X | | X | |
| *Rhopalodia gibba* | X | | | | | X |
| *Stauroneis anceps* | | X | | | | |
| *Stauroneis anceps* var. *gracilis* | | | X | | | |
| *Stauroneis phoenicentron* | | X | | | | X |
| *Stephanodiscus astrea* var. *minutula* | X | | | X | | |
| *Stephanodiscus dubius* | X | | | | X | |
| *Surirella ovalis* | X | | | | X | |
| *Tabellaria fenestrata* | | | X | | | X |
| *Tabellaria flocculosa* | | | X | | | X |

Column numbers identify the following pH and saprobien conditions.

1. Alkaliphilous
2. Indifferent
3. Acidophilous
4. Saproxenous
5. Oligosaprobic
6. Mesosaprobic

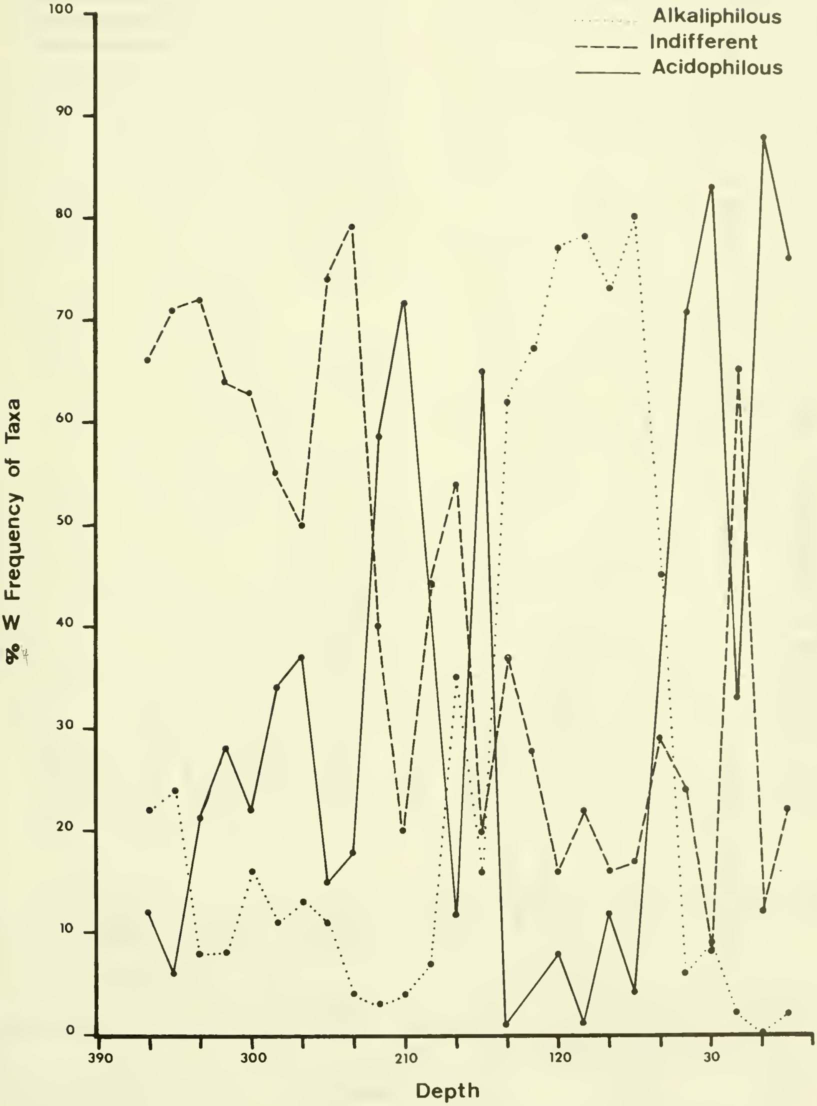

Fig. 7. Percent sum frequency of known alkaliphilous, pH indifferent, and acidophilous diatoms in relation to sediment depth.

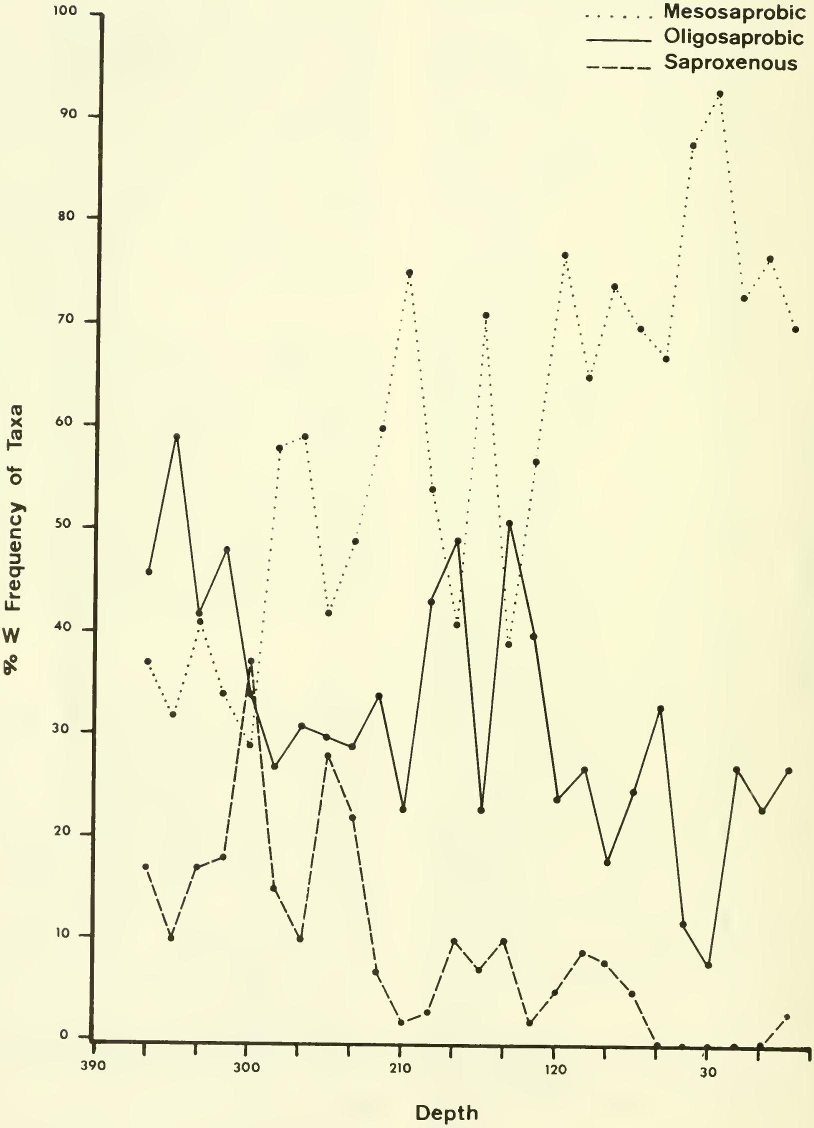

Fig. 8. Percent sum frequency of known mesosaprobic, oligosaprobic, and saproxenous diatoms in relation to sediment depth.

resulted in two depositional units separated by a minor erosional unconformity. $C^{14}$ dates suggest deposition of the lower unit between about 3,100 and 1,800 years B.P. and deposition of the upper unit between about 1,800 and 1,000 years B.P. The younger advances of Neoglaciation represent the Gannett Peak Stade. Historic records show that the glaciers abutted the moraines of the Gannet Peak Stade as recently as about 1850, and this moraine was very extensive. According to Richmond's observations (1965) the mean summer temperature during late Pleistocene glacial maxima was about 16 F (8 C) colder than at present in the southern Rocky Mountains and 17.5 F (9 C) colder in the northern Rocky Mountains. Winter temperatures then were much the same as at present.

Similarly Martin (1963) has studied pollen stratigraphy from desert regions of southwestern North America. Based on changes in pollen composition through time, he discussed climatic changes over the last 10,000 years. He inferred three major features of postpluvial climatic history of southwestern America: an initial arid period climatically equivalent to the present and dating 8,000–10,500 years B.P.; a less arid interval with an intensified monsoon rainfall, the climate perhaps no warmer but wetter than at present and corresponding in time to the classic "altithermal" of 4,000 to 8,000 years B.P.; and finally an arid period closely resembling present conditions (with one possible shift in the seasonal distribution of rainfall) lasting from 4,000 B.P. to the present.

Morrisson and Frye (1965) studied shore line changes of Lake Bonneville and Lake Lahonton. Based on these and other observations, they concluded that glacial advances and retreats were nearly synchronous with rises and falls of these lakes.

It is difficult to use such studies as these to infer paleoclimatic conditions at Lily Lake. However, it seems likely that this lake was formed during the last major glacial retreat in the Uinta Mountains (Atwood 1909). A glacier at that time apparently scoured an extant lake basin or formed a new basin which became Lily Lake. This likely occurred 12,000–10,000 years B.P. corresponding to the end of Pinedale glaciation (Richmond 1965) and the retreat of Lake Bonneville. This assumption is made since Lily Lake is at sufficient elevation and is in a geographical position to be scoured by each new major glacial advance, and it appears that the last major Uinta Mountain glaciation corresponds to Pinedale glacial times in the Rocky Mountains. Likewise, rises in elevation of Lake Bonneville (Great Salt Lake) have not been prominent during the past 10,000 years.

If deposition was uniform throughout the history of Lily Lake, the period of disturbance noted in the core around 225–150 cm (Table 5) lies between approximately 8,000–4,000 years B.P. This corresponds to zone III of Martin (1963), which was characterized by intensified rainfall. This tends to support our hypothesis that increased precipitation and consequent flushing of Lily Lake interrupted the development of strictly dystrophic conditions that began at about the 225 cm level, causing a return to oligo-mesotrophic conditions.

Table 5 summarizes the results of four analyses of the diatom data from our core. In all cases the disturbance zone is evident.

Table 5. Summary of results of different analyses in reference to diatom floral changes in Lily Lake with core depth. The lake stages shown on the left were identified via floristic data. The sediment depth figures represent depths of the peat through which the lake stages were extant according to each analysis technique.

| Identified Lake Stages | Analysis Technique | | | |
|---|---|---|---|---|
| | Stand cluster | Diversity changes | pH preference changes | Saprobic changes |
| | | Depth Below Current Sediment Surface (cm) | | |
| Oligo-mesotrophic | *360-240 | 360-225 | 360-225 | 360-225 |
| Dystrophy-Disturbance | 225-180 | 225-135 | 225-150 | 225-135 |
| Oligo-mesotrophic | 150-75 | 135-60 | 150-60 | 135-60 |
| Dystrophy | 60-0 | 60-0 | 60-0 | 60-0 |

*Figures represent depths of peat from surface.

Future floristic and ecological studies of other bog lakes in the Uinta and other mountains of Utah, together with radiocarbon dating of sediments, are planned. We hope to correlate these studies with palynological studies to aid our understanding of paleoclimatology.

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# VEGETATIONAL RESPONSE TO THREE ENVIRONMENTAL GRADIENTS IN THE SALT PLAYA NEAR GOSHEN, UTAH COUNTY, UTAH

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Abstract.— The plant communities and individual plant species in and around a salt playa near Goshen, Utah County, Utah, were studied in relation to gradients for soluble salts, soil moisture, and pH. Forty-eight stands were sampled. Frequency data were taken for all plant species. Soil samples were collected from each site and analyzed to establish the environmental gradients.

Results indicate that the vegetational types respond differentially to the three gradients and can be segregated on the basis of one or more of the gradients. The total soluble salts gradient was found to be the most influential of the three sampled. Correlation analysis indicates that 45 percent of the variation in plant diversity can be accounted for by the three gradients. Distributional patterns of individual plant species are strongly influenced by the three gradients. Niche width measurements exhibited no correlation with the measured gradients.

The study area is at the southern end of Utah Lake, south of Goshen Bay, in Central Utah (Fig. 1). Due to lack of drainage, much of the low-lying land in this area has high concentrations of soluble salts. Depressions in the area accumulate sufficient salt to totally suppress plant growth and become barren playas. Surrounding the playas, zones of vegetation form discrete plant associations with narrow ecotones (Fig. 1). The most salt tolerant or salt dependent types grow closest to the playas. Away from the playa and in the direction of higher ground, the vegetation becomes progressively less salt tolerant.

A general description of the climate near Goshen is given by Hansen (1974). Temperatures were shown to gradually increase through May and June, with July having an average daily high of 34 C. Daily mean relative humidity was lowest from mid-July through mid-August. Relative humidity (except for six evenings) reached 100 percent every night during the growing season. Growing season precipitation was confined to two seasons, the first in late May through early June and the second in late August through early September.

Based upon growth ring analysis of the woody stems of *Allenrolfea occidentalis*, Hansen and Weber (1975) concluded that the study area has become more moist in the last 35 years. They attributed this change in soil moisture to increased surface and subsurface water from irrigation of nearby fields.

The effect of saline and alkali substrates on plants has been studied by several authors. Magistad (1945) reviewed over 350 papers dealing with plant growth on saline and alkali soils. Waisel (1972) outlined some of the major problems facing plants growing in hydromorphous salt playas. In his discussion, Waisel recognized high salinity, low partial pressure of oxygen, high carbon dioxide concentrations, and altered oxidation-reduction relations as major problems. Magistad (1945) differentiated between the effects of saline and alkali soils on plant growth. Saline soils reduced plant growth by increasing osmotic potential of the soil solution. On alkali soils, however, plant growth was affected by reduced soil permeability, lack of oxygen, malnutrition, cholorosis, and even corrosive action.

In arid regions the most crucial factor limiting plant growth is available water, and salinity is considered the second most limiting variable (Chapman 1966). The largest area of salt-affected soils combine both adverse features—salinity and aridity. Plants native to such areas combine adaptations which ameliorate the effects of osmotic withdrawal of water and sodium (and other ion) toxicity (Dregne 1963). The most important factor affecting plant distribution in saline soils is the

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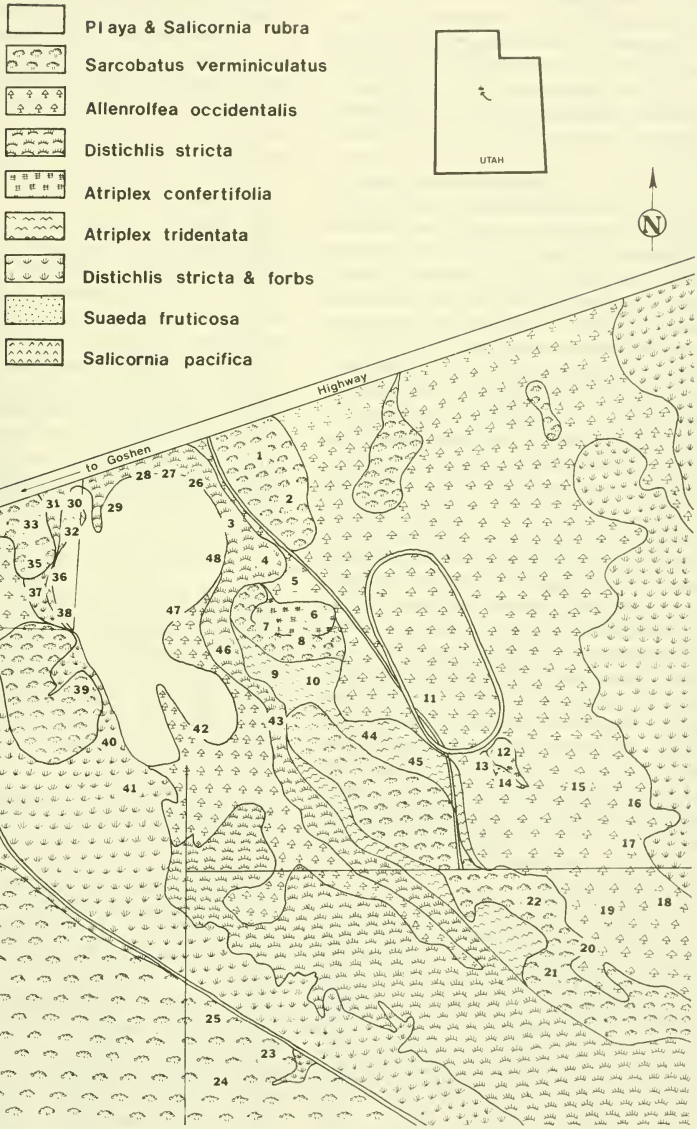
Playa & Salicornia rubra
Sarcobatus verminiculatus
Allenrolfea occidentalis
Distichlis stricta
Atriplex confertifolia
Atriplex tridentata
Distichlis stricta & forbs
Suaeda fruticosa
Salicornia pacifica
UTAH
N
Highway
to Goshen
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2
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g. 1. Vegetation map of the study area illustrating vegetation distribution patterns and location of study plots.

osmotic concentration of the soil solution (Ungar, Hogan, and McClelland 1969, Waisel 1972, Al-Jibury 1972).

Chapman (1966) indicated that the zonation patterns of plant communities growing around saline areas were related to soil salinity. The salinity was expressed by the amount of sodium chloride or soluble chloride present in the soil or in terms of osmotic pressures.

The effects of hydrogen ion concentration on plants are not well known, but include alterations in nutrient availability and/or toxicity (Kramer 1956) and disease susceptibility (Daubenmire 1959). The availability of manganese, iron, copper, molybdenum, and zinc in a soil tends to decline as pH values rise above 7.0 (Buckman and Brady 1969). In regard to plant distribution, Olsen (1924) concluded that soil hydrogen ion concentration affected plant cover. This was, however, refuted by Daubenmire (1959), who stated that pH was not as closely correlated with biological phenomenon as formerly believed. Ungar, Hogan, and McClelland (1969) found that the range of hydrogen ion concentration tolerated by plant communities and species was broad. Their findings indicate that hydrogen ion concentration was probably not one of the environmental factors exerting a strong influence on species distribution.

Studies concerning indicator significance of desert shrubs have been conducted by a number of authors. In a study of plant distribution in the Escalante Desert of Utah, Lambert (1940) found a definite correlation between soil alkalinity and plants found growing under various conditions of alkalinity. Harris (1920) compiled a list of indicator plants and described the soil conditions they indicated.

In a study of the indicator significance of some shrubs in the Escalante Desert of Utah, Fireman and Hayward (1952) described the distribution of *Sarcobatus vermiculatus*, *Atriplex confertifolia*, and *Artemisia tridentata* stands in relationship to soil pH and exchangeable sodium. They found that the distribution of these plants was correlated with the pH and exchangeable sodium concentration of the soil.

Fautin (1946), in a study of the northern desert shrub biome in Utah, outlined the general soil and moisture requirements of a number of the plant species involved. Gates, Stoddart, and Cook (1956) found local soil variations insufficient to explain the distribution of the different plant communities on the salt desert of Utah. Goodman (1973) and Goodman and Caldwell (1971) attempted to explain mosaic patterns of dominant salt desert plant communities and their subdominants on the basis of ecotypic variation rather than on the basis of soil chemistry.

In a study of the flora of the Great Salt Lake region of Utah, Flowers and Evans (1965) described the vegetation of the saline and nonsaline areas around Great Salt Lake. They found the vegetation in distinct patterns around the salt playas. They attributed the patterns to increasing salt concentrations toward the center of the playas. The following sequence was determined for plant invasion of playas (plants are listed in order of decreasing tolerance to soil salinity): 1) *Salicornia rubra* or *Salicornia pacifica*, 2) *Suaeda erecta*, 3) *Allenrolfea occidentalis*, 4) *Distichlis spicata*, and 5) *Suaede fruticosa*.

## METHODS AND MATERIALS

Forty-eight 10 × 10 m study plots of homogenous vegetation were sampled within the major vegetation zones. Eight meter-square quadrats were located at random within each study plot, and species frequency data were taken. Quadrat frequency was computed for all species in each plot (Phillips 1959).

A Constancy times Frequency (C × F) Index (Anderson 1964, Curtis 1959) was computed for all plant species in the study (Table 1). This index gives an indication of the relative importance of each species in the community. For instance, *Salicornia rubra*, with a C × F Index of 2278 would be the most widespread species in the study area (Table 1).

Soil samples were collected during the third week of August. This was considered the time when soil moisture values would exhibit maximum differential between the driest and the most moist habitats (Hansen 1975). This differential was enhanced by the fact that there had not been any precipitation in the area for three weeks preceding the collection of data. Soils were collected only once during the growing season, since only the relative magnitude between community differences for the various soil parameters was required for our purposes.

The soil samples were collected from two soil pits dug at each study plot. Samples were taken from the surface inch, 6- to 12-inch level, and the 18-inch level. Samples were analyzed in the laboratory for total soluble salts, hydrogen ion concentration, and percent soil moisture. Total soluble salts were determined by means of a Beckman model RC216B2 conductivity bridge. Hydrogen ion concentration was determined using a glass electrode Sargent-Welch pH meter. Percent soil moisture was determined by weighing fresh soil samples, drying for 48 hours at 110 C, and then reweighing.

TABLE 1. Species listed in order of decreasing constancy times frequency (C × F) index numbers

| Species | C × F Index | Percent constancy | Average frequency |
|---|---|---|---|
| *Salicornia rubra* | 2278 | 54 | 42.2 |
| *Distichlis spicata* | 1250 | 50 | 25.0 |
| *Lepidium perfoliatum* | 1154 | 38 | 30.4 |
| *Allenrolfea occidentalis* | 1100 | 44 | 25.0 |
| *Bromus tectorum* | 842 | 33 | 25.5 |
| *Suaeda fruticosa* | 460 | 31 | 14.8 |
| *Sarcobatus vermiculatus* | 288 | 23 | 12.5 |
| *Atriplex confertifolia* | 218 | 21 | 10.4 |
| *Salicornia pacifica* | 202 | 21 | 9.6 |
| *Kochia americana* | 137 | 21 | 6.5 |
| *Atriplex tridentata* | 125 | 13 | 9.6 |
| *Triglochin maritima* | 113 | 16 | 7.0 |
| *Sueda depressa* | 57 | 13 | 4.4 |
| *Cordylanthus canescens* | 26 | 10 | 2.6 |
| *Descurainia sophia* | 23 | 6 | 3.9 |
| *Poa nevadensis* | 20 | 8 | 2.6 |
| *Haplopappus lanceolatus* | 20 | 8 | 2.6 |
| *Chenopodium album* | 20 | 8 | 2.3 |
| *Puccinellia airoides* | 13 | 8 | 1.6 |
| *Atriplex patula* | 10 | 8 | 1.0 |
| *Sitanion hyxtrix* | 7 | 6 | 1.2 |
| *Opuntia polyacantha* | 7 | 6 | 1.2 |
| *Chrysothamnus nauseosus* | 3 | 4 | .8 |
| *Agropyron smithii* | 3 | 2 | 1.3 |
| *Poa sandbergii* | 2 | 4 | .5 |
| *Sporobolus airoides* | 2 | 4 | .5 |
| *Salsola iberica* | 2 | 2 | .8 |
| *Camelina microcarpa* | 2 | 4 | .5 |
| *Artemisia tridentata* | 1 | 2 | .3 |

Soil data from the three depth horizons and the two pits per site were averaged (to obtain values used in the establishment of the environmental gradients for total soluble salts, hydrogen ion concentration (to obtain a workable gradient for hydrogen ion concentration, pH values were carried out to hundredth of a pH unit), and percent soil moisture (Beadle, Whalley, and Gibson 1957). Stands common to a portion of the gradient were combined for analytical purposes, and average frequency values for participating species within each group were computed (Table 2).

After stands common to a portion of the gradient were combined, the response of individual species and of combinations of species of common growth form (i.e., shrubs, grasses, annuals, species with succulent stems, forbs, and perennials) were graphed (using frequency data as the criterion of performance) against the environmental gradient to display distribution trends (Figs. 2–4). Average percent frequency values for all plant species were computed for all plots assigned to each segment of the gradient. Average values based upon all plots common to a given segment of the gradient shows smoother

TABLE 2. Characteristics of the study sites included in each segment of the soluble salts, soil moisture, and pH gradients.

| | Total soluble salts in p.p.m. | | | Soil moisture as percent of dry weight | | | Hydrogen ion concentration (pH) | | |
|---|---|---|---|---|---|---|---|---|---|
| Groups | Lower boundary | Upper boundary | Mean[*] | Lower boundary | Upper boundary | Mean[*] | Lower boundary | Upper boundary | Mean[*] |
| 1 | 636 | 879 | 732 | 3.1 | 10.2 | 8.0 | 8.17 | 8.27 | 8.22 |
| 2 | 934 | 1,686 | 1,263 | 10.5 | 13.4 | 12.3 | 8.32 | 8.43 | 8.38 |
| 3 | 3,266 | 4,901 | 4,176 | 15.0 | 18.0 | 16.5 | 8.47 | 8.54 | 8.51 |
| 4 | 9,522 | 13,152 | 11,159 | 18.6 | 19.9 | 19.2 | 8.55 | 8.59 | 8.56 |
| 5 | 14,906 | 19,096 | 16,577 | 20.5 | 22.4 | 21.2 | 8.62 | 8.70 | 8.67 |
| 6 | 22,819 | 22,152 | 24,090 | 23.1 | 26.5 | 24.6 | 8.79 | 8.88 | 8.83 |
| 7 | 26,008 | 27,037 | 26,543 | 27.5 | 32.0 | 29.7 | 9.03 | 9.04 | 9.03 |

[*] Mean is an expression of the average values for all stands included in the group.

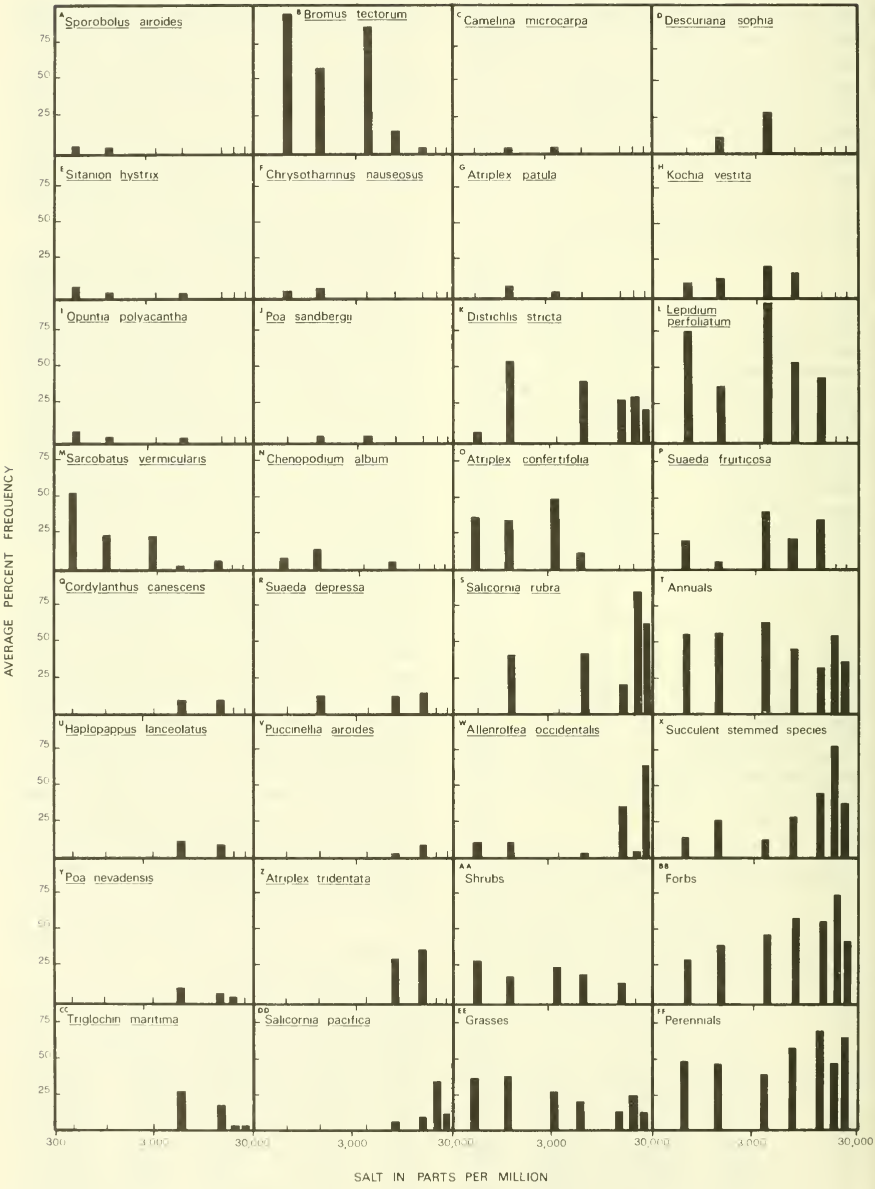

Fig. 2. Individual plant species and growth form response to soil soluble salts concentration in the soil.

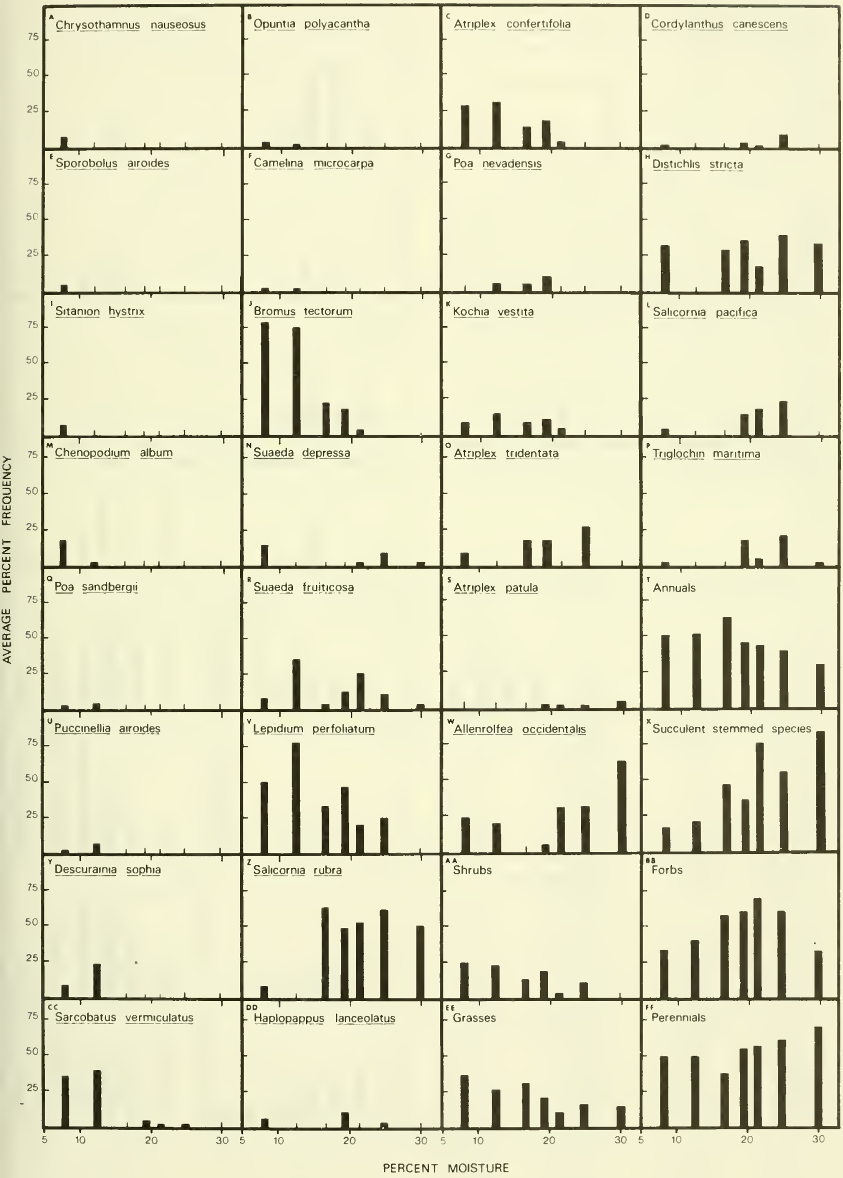

Fig. 3. Response of individual plant species and growth form response to the soil moisture.

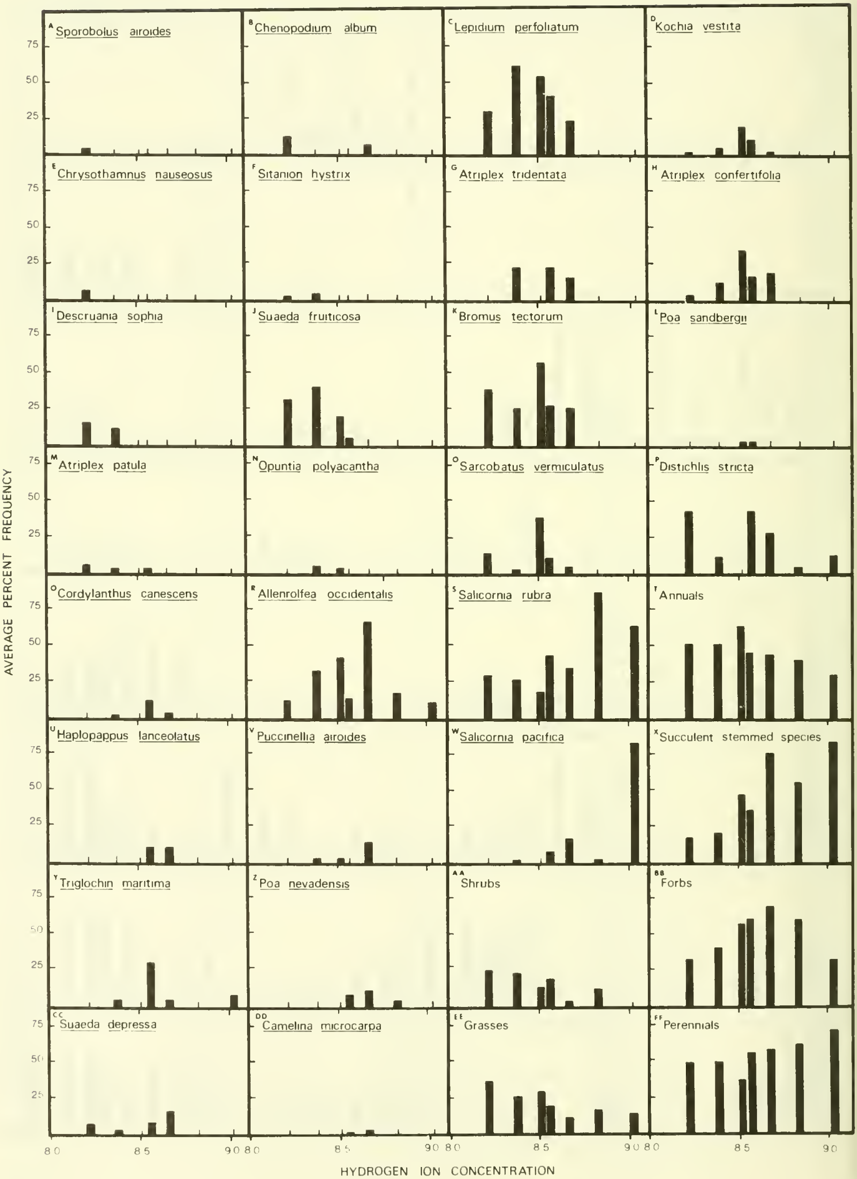

Fig. 4. Response of individual plant species and growth forms to soil pH.

trends along the gradient for any variable than do individual values for that variable at each plot (Bross 1974).

Stand diversity and species niche width values were computed from frequency data using the equation:

$$B = \frac{1}{\Sigma pi^2}$$

where "B" is equal to either the species niche width or stand diversity, and "pi" is a measure of the relative abundance of a species in a given habitat (Levins 1966, MacArthur 1972). Species niche width values were obtained by summing "pi" values across all stands. Stand diversity values were obtained by summing "pi" values for all species found within a given stand.

Total soluble salts, hydrogen ion concentration, and percent soil moisture preference indices (Table 3) were computed for all participating species by the following equation:

$$\text{Preference Index} = \frac{\text{Frequency of species A times the gradient value of the stand in which it occurs}}{\text{Frequency values of species A across all stands in which it occurs}}$$

This was done in an attempt to facilitate comparison of species niche width values and their general distribution patterns along the total soluble salts, hydrogen ion concentration, and percent soil moisture gradients.

Correlation analyses (Hall 1971, Dick 1971) were conducted to determine the degree to which the different gradients were associated, and the degree to which species niche width value and stand diversity indices were controlled and/or affected by the measured gradient factors (Tables 4 and 5). Multiple regression analysis (Snedocor and Coch-

TABLE 3. Species niche width (N.W.), salt preference (S.P.), hydrogen ion concentration preference (H.P.), and moisture preference (M.P.) index numbers, in order of niche width.

| Species | N.W. | S.P. | M.P. | H.P. |
|---|---|---|---|---|
| *Agropyron smithii* | 1.00 | 639.00 | 3.11 | 8.19 |
| *Artemisia tridentata* | 1.00 | 639.00 | 3.11 | 8.19 |
| *Salsola iberica* | 1.00 | 639.00 | 3.11 | 8.19 |
| *Chrysothamnus nauseosus* | 1.82 | 835.67 | 4.04 | 8.22 |
| *Camelina microcarpa* | 2.00 | 2,711.65 | 11.16 | 8.63 |
| *Poa sandbergii* | 2.00 | 3,029.00 | 11.38 | 8.53 |
| *Sprobolus airoides* | 2.00 | 786.50 | 3.81 | 8.22 |
| *Chenopodium album* | 2.64 | 4,441.44 | 5.57 | 8.32 |
| *Opuntia polyacantha* | 2.70 | 3,614.25 | 13.26 | 8.41 |
| *Sitanion hyxtrix* | 2.70 | 3,960.90 | 11.89 | 8.46 |
| *Descurainia sophia* | 2.77 | 3,053.75 | 10.81 | 8.29 |
| *Haplopappus lanceolatus* | 2.80 | 12,447.90 | 17.57 | 8.60 |
| *Poa nevadensis* | 2.95 | 15,183.80 | 16.79 | 8.65 |
| *Puccinellia airoides* | 3.04 | 18,200.17 | 15.81 | 8.57 |
| *Atriplex patula* | 3.62 | 5,539.30 | 24.13 | 8.34 |
| *Atriplex tridentata* | 4.60 | 16,711.27 | 20.44 | 8.49 |
| *Triglochin maritima* | 4.72 | 14,185.63 | 22.47 | 8.59 |
| *Cordylanthus canescens* | 4.82 | 13,438.70 | 22.23 | 8.56 |
| *Suaeda depressa* | 5.06 | 12,196.93 | 17.96 | 8.52 |
| *suaeda fruticosa* | 5.83 | 9,542.13 | 18.09 | 8.47 |
| *Salicornia pacifica* | 7.42 | 23,015.97 | 21.46 | 8.90 |
| *Kochia americana* | 7.75 | 7,348.80 | 15.69 | 8.51 |
| *Atriplex confertifolia* | 8.53 | 3,339.07 | 13.75 | 8.51 |
| *Bromus tectorum* | 13.83 | 3,954.18 | 12.08 | 8.45 |
| *Allenrolfea occidentalis* | 14.93 | 22,558.37 | 21.49 | 8.55 |
| *Lepidium perfoliatum* | 17.48 | 6,646.18 | 15.14 | 8.44 |
| *Distichlis spicata* | 21.40 | 14,827.39 | 20.05 | 8.58 |
| *Salicornia rubra* | 23.13 | 20,393.93 | 21.79 | 8.90 |
| *Sarcobatus vermiculatus* | 29.76 | 3,126.67 | 10.59 | 8.46 |

ran 1967) was conducted to determine the combined influenced of pH, salinity, and soil moisture on stand diversity and species niche width.

## Results and Discussion

The response of the plant communities to the soluble salts gradient was generally clear-cut. All community types segregate along the gradient: however, the most clearly defined segregations occurred among those stands dominated by halophytic species.

With the exception of stand 34 (Fig. 1), which exhibited 13,095 ppm total soluble salts, all of the stands of *Allenrolfea occidentalis* exhibited total soluble salts concentrations between 26,401 and 27,037 ppm. Stands dominated by *Salicornia rubra* were found to occur from 22,819 ppm total soluble salts to 26,909 ppm. *Salicornia rubra* also occurred as a subdominant in the *Distichlis spicata* stands which exhibited salt concentrations of around 10,468 ppm. The stands of *Salicornia pacifica* were found to occur in soils with 24,265 to 26,407 ppm total soluble salts.

Table 4. Correlation of environmental gradients with each other and with the plot diversity indices. Given are "r" and "$r^2$" values and levels of significance (n = 48). Multiple regression analysis of all three environmental gradients versus diversity index values results in "$R^2$" = .45.

| Variables correlated | "r" | "$r^2$" | Significance level |
|---|---|---|---|
| Salt-moisture | .3811 | .15 | .01 |
| Salt-pH | .1080 | .01 | N.S. |
| Moisture-pH | –.7813 | .61 | .01 |
| Salt-diversity index | –.6068 | .37 | .01 |
| Moisture-diversity index | –.3766 | .14 | .01 |
| pH-diversity index | –.0113 | .0001 | N.S. |

Table 5. Correlation of species preference indices for three variables with each other or with niche width values. Given are "r" and "$r^2$" values and levels of significance (n = 29). Multiple regression analysis of all three preference indices versus niche width results in "$R^2$" = .11.

| Variables correlated | "r" | "$r^2$" | Significance level |
|---|---|---|---|
| Salt-Moisture | .2509 | .06 | N.S. |
| Salt-pH | .4134 | .17 | .05 |
| Moisture-pH | –.6829 | .47 | .01 |
| Salt-N.W. | .2756 | .08 | N.S. |
| Moisture-N.W. | .0526 | .003 | N.S. |
| pH-N.W. | .2025 | .04 | N.S. |

Along the lower end of the salt gradient there was less obvious order. A great deal of overlap occurred between the plant communities on that portion of the gradient. *Sarcobatus-Atriplex* stands exhibited ranges of from 635 to 11,226 ppm total soluble salts. Stands of *Atriplex confertifolia* were found on plots having from 772 to 4,900 ppm salts. Stands dominated by *Suaeda fruticosa* were found in soils where salt concentrations ranged from 3,266 to 15,619 ppm. *Atriplex tridentata* stands occurred in soils which exhibited total soluble salts concentrations ranging from 9,255 to 18,506 ppm.

*Distichlis spicata* communities tended to be the least restricted of any of the communities found along the gradient. Stands of *Distichlis spicata* exhibited ranges in soluble salt concentration of 1,211 to 26,533 ppm.

In comparison to the total soluble salts gradient, the soil moisture gradient produced maximum segregation of plant species at lower moisture levels. Stands of *Sarcobatus vermiculatus* and *Atriplex confertifolia*, both in pure stands and in association with each other, were found primarily at the low moisture end of the gradient. With the exception of one stand, all communities of *Sarcobatus vermiculatus* and its codominants were found in soils with less than 12 percent soil moisture. *Atriplex confertifolia* stands occurred in soils showing between 10 and 19 percent moisture. Stands of *Suaeda fruticosa* were found along the moisture gradient in soils having 12 to 21 percent moisture. *Allenrolfea occidentalis* stands occurred in soils having between 10 and 31 percent moisture. *Salicornia rubra* communities were found to occupy the middle portions of the moisture gradient and occurred in soils which exhibited a range of 15 to 20 percent moisture. *Salicornia pacifica* stands occurred next to *Salicornia rubra* stands on the soil moisture gradient and occupied areas exhibiting 18 to 23 percent soil moisture.

The hydrogen ion concentration (pH) gradient, like the salt and moisture gradients, affected some community types more than others. Stands dominated by either *Salicornia rubra* or *Salicornia pacifica* were those most strictly segregated along the hydrogen ion concentration gradient. *Salicornia rubra* dominated stands were all found between pH values of 8.79 and 8.88. As a co-dominant with *Distichlis spicata*, however, *Salicornia rubra* grew in soils exhibiting a pH of 8.41. The plant communities occurring in soils with a mean pH of 9.0 or greater were all dominated by *Salicornia pacifica*. The stands dominated solely by the two species of *Salicornia* were found to exhibit the narrowest pH ranges of all stands studied.

Other stands exhibited much broader pH ranges. Stands of *Suaeda fruticosa*, for example, were found to occupy areas with pH values between 8.17 and 8.35 mean soil pH. There were no stands dominated solely by *Sarcobatus vermiculatus* included in this study. It was always found growing with co-dominates (i.e., *Agropyron smithii*, *Chrysothamnus nauseosus*, and *Atriplex confertifolia*). *Atriplex tridentata* stands occurred in areas where mean pH values ranged from 8.34 to 8.59. *Allenrolfea occidentalis* stands exhibited variations in mean pH values of 8.42 to 8.69.

*Distichlis spicata* communities again exhibited wide tolerance ranges for gradient values (i.e., pH levels from 8.24 to 8.59) and thus seemed to be the least restricted by hydrogen ion concentrations in the soil of the communities studied.

The results of correlation and multiple regression analyses between gradients are found in Table 4. The salt and moisture gradients correlated at a significance level of .01 with an "$R^2$" of 0.61. Diversity Index values correlated with salt at the .01 level of significance and an "$R^2$" of .37, with moisture also at the .01 level of significance with an "$R^2$" of .14; and with hydrogen ion concentration the correlation was nonsignificant. The multiple regression analysis of Diversity Indices and all three gradients yielded an "$R^2$" value of .45.

The response of individual plant species and selected plant growth forms to the three gradients were studied by plotting the average percent frequency of each species or vegetation type against each of the three gradients. Figures 2 through 4 represent the results.

Figure 2 shows the response of individual plant species to total soluble salts. *Sporobolus airoides*, *Sitanion hystrix*, *Opuntia polyacantha*, *Chrysothamnus nauseosus*, and *Bromus tectorum* can be classified as having low tolerance to salt. Species which exhibited their greatest frequencies between 934 and 13,152 ppm total soluble salts were classified as moderately tolerant. These species included *Poa sandbergii*, *Chenopodium album*, *Camelina microcarpa*, *Atriplex patula*, *Distichlis spicata*, *Atriplex confertifolia*, *Sarcobatus vermiculatus*, *Descuraninia sophia*, *Kochia americana*, and *Lepidium perfoliatum*. Tolerant species were those which exhibited their greatest frequencies on sites having between 14,906 and 25,152 ppm total soluble salts. Included in this classification were *Suaeda fruticosa*, *Cordylanthus canescens*, *Haplopappus lanceolatus*, *Poa nevadensis*, *Triglochin maritima*, *Suaeda depressa*, *Puccinellia airoides*, *Atriplex tridentata* and *Salicornia pacifica*. Species which exhibited their greatest frequencies in soils with salt concentrations in excess of 26,008 ppm were classified as highly tolerant. *Allenrolfea occidentalis* and *Salicornia rubra* were classified in this group. Only the extremely high salt concentrations of the playa were limiting to these two species, which tolerated conditions on the edge of the playas. This response of various plant growth forms to the salt gradient are shown in Figure 2. Shrubs and grasses decreased as total soluble salts increased. Forbs increased with total soluble salt up to about 25,152 ppm and then decreased. Perennials increased slightly as total soluble salts increased. Succulent stemmed species increased rapidly at higher total soluble salts concentrations. Annuals exhibited little response to the salt gradient.

Individual plant species response to soil moisture is shown in Figure 3. *Chrysothamnus nauseosus*, *Sporobolus airoides*, and *Sitanion hystrix* were restricted to the most xeric portions of the soil moisture gradient. *Opuntia polyacantha*, *Camelina microcarpa*, *Puccinellia airoides*, *Poa sandbergii*, and *Descurainia sophia* were generally restricted to areas from 3 to 13 percent soil moisture, although *Opuntia polyacantha* did appear at a very low average frequency between 20 and 22 percent soil moisture. *Sarcobatus vermiculatus* and *Atriplex confertifolia* were most frequent from 3 to 13 percent soil moisture, but *Sarcobatus vermiculatus* was found in soils having up to 26 percent moisture and *Atriplex confertifolia* in soils having up to 22 percent moisture. The range of *Salicornia rubra* along the soil moisture gradient was from 3 to 32 percent. However, it exhibited very high average frequency from 15 to 31 percent soil moisture. *Poa nevadensis* was restricted along the soil moisture gradient to soils with 11 to 20 percent moisture content. *Atriplex tridentata* increased in average frequency as soil moisture increased from 3 to 25 percent moisture. *Kochia americana* was restricted to areas of less than 22 percent soil moisture. *Salicornia pacifica* and *Trilochin maritima* exhibited their greatest average frequencies from 19 to 26 percent soil moisture. *Salicornia pacifica* was found from 3 to 26 percent soil moisture and *Triglochin maritima* was found in soils with 3 to 31 percent soil moisture. *Atriplex patula* was restricted to soils exhibiting from 19 to 32 percent moisture and was most frequent in the more mesic portions of the gradient. *Allenrolfea occidentalis* occurred all along the soil moisture gradient from 3 to 32 percent, but was most successful in the more mesic soils.

Several species exhibited little response to the soil moisture gradient. *Suaeda depressa* occurred along the gradient in soils which exhibited from 3 to 31 percent and did not exhibit any area of optimum response. *Suaeda fruticosa* had a range of soil moisture from 3 to 32 percent. *Haplopappus lanceolatus* and *Cordalanthus canescens* were found in soils exhibiting 3 to 26 percent moisture. As with the total soluble salts gradient, *Distichlis spicata* was found most ubiquitously across the soil moisture gradient, from 3 to 32 percent moisture.

The plant growth forms responded to moisture with essentially the same patterns as they displayed for total soluble salts. Shrubs, grasses, and annuals all declined in average frequency as moisture increased. Succulent stemmed species increased rapidly with increasing soil moisture. Forbs increased to a point near the most mesic end of the gradient and then declined rather rapidly. Perennials increased somewhat with increasing soil moisture.

The responses of the individual plant species to the hydrogen ion concentration gradient are shown in Figure 4. Species were classified as being of low, moderately tolerant, tolerant, and highly tolerant in response to soil alkalinity. Species which exhibited low tolerance to increasing alkalinity in the soil were *Sporobolus airoides, Chrysothamnus nauseosus, Descurainia sophia, Atriplex patula* and *Sitanion hystrix.* Moderately tolerant species were those with their greatest average frequencies between pH 8.17 and 8.54. These species were *Suaeda fruticosa, Opuntia polyacantha, Lepidium perfoliatum, Atriplex tridentata, Bromus tectorum, Sarcobatus vermiculatus, Kochia americana, Atriplex confertifolia,* and *Poa sandbergii.* Species which exhibited their greatest average frequencies along the hydrogen ion concentration gradient between 8.55 and 8.88 were tolerant species. Species classified as tolerant were *Distichlis spicata, Cordylanthus canescens, Haplopappus lanceolatus, Triglochin maritima, Suaeda depressa, Allenrolfea occidentalis, Puccinellia airoides, Poa nevadensis,* and *Camelina microcarpa.* Highly tolerant species were *Salicornia rubra* and *Salicornia pacificia,* which exhibited their greatest average frequencies in soils with pH values over 9.00.

The plant growth form responses to the hydrogen ion concentration gradiant can also be observed in Figure 4. Shrubs responded to hydrogen ion concentration along a modified "bell-shaped" curve. That is, the average frequencies of the shrubs were greatest in the middle of the gradient and tapered downward toward either end of the gradient. Grasses and annuals exhibited little response to the alkalinity gradient. Succulent stemmed species responded to the hydrogen ion concentration gradient in a manner very similar to their responses to the salt and moisture gradients. That is, they increased at an accelerating rate across the gradient. Forbs exhibited a "U-shaped" response to increasing pH values. Perennials, like succulent stemmed species, responded to the hydrogen ion concentration gradient in a manner similar to their response to salts and soil moisture.

Table 5 contains the results of the correlation analysis between niche width values and the preference index values of the plant species studied. Niche width was not significantly correlated to any of the three species preference indices. There was a nonsignificant correlation between salt and moisture preference values. Salt and hydrogen ion concentration correlated at the 0.05 level of significance with an "$R^2$" of .17. Moisture and hydrogen ion concentration were negatively correlated at the 0.01 level of significance with an "$R^2$" of .47. The multiple regression analysis of niche widths and species preference indices was nonsignificant.

The Goshen salt playa is typical of a great number of small playas found in the area south of Utah Lake. The vegetation surrounding the playa ranges from halophytes immediately surrounding the playa to nonhalophytes (glycophytes) on the small knolls adjacent to the playa. Transition zones between the various plant communities were characteristically sharp; plant communities nearest the playa exhibited the narrowest ecotones. The plant species responded to various environmental gradients and tended to sort themselves into discreet plant communities. The sharp zonation patterns were also noted by Flowers and Evans (1965). They attributed the narrow ecotones to the increasing gradient of salt concentration toward the center of the playa.

Table 1 is a species list with the species arranged in order of decreasing Constancy times Frequency (C × F) Index values. The C × F Index is used as a measure of the relative importance of a particular species across the entire system of communities. Those species exhibiting higher C × F Index values were, in this study, generally the most salt tolerant (i.e., *Salicornia rubra Distichlis spicata, Allenrolfea occidentalis*). The effects of cattle grazing and other disturbance on the area were evidenced by the relative importance of two introduced species, *Lepidium perfoliatum* and *Bromus tectorum.*

Of the three environmental factors studied, total soluble salts appeared to be the most important factor regulating the distribution patterns of the various plant communities studied. Although each of the factors studied exhibited an effect on some or all of the communities sampled, total soluble salts were the most restrictive, particularly at high concentrations. Moisture seemed to exhibit the least effect upon the segregation of the various communities, as there was little order and a great deal of overlapping of the moisture values of the stands studied. The hydrogen ion concentration of the soil was quite restrictive to some of the communities. For instance, stands of *Salicornia rubra* and *Salicornia pacifica* were all restricted to sites having high pH levels. Because both of these species occurred as co-dominants with other species in communities exhibiting lower levels of hydrogen ion concentration, it was felt that areas dominated by these species are habitat types not environmentally suitable to other plants, which at lower pH ranges tended to out-compete the *Salicornia* species. It might also be that, where these two species are found within other vegetation types, microhabitat relationships may well echo the habitats they dominate.

The three gradients did not exhibit particularly close correlation (Table 4). The general lack of high degrees of correlation between the three gradients indicates that the gradients functioned somewhat independently of one another. The correlation coefficients, significance levels and "$R^2$" values indicate that soluble salts and moisture gradients influenced most strongly the species diversity in the plant communities considered in this study. Hydrogen ion concentration, however, exerted little or no influence on the diversity of the stands sampled.

A multiple regression analysis of the three environmental factors versus the diversity index yielded an "$R^2$" value of .45. This would indicate that about 45 percent of the diversity exhibited by the stands studied can be accounted for by variation in total soluble salts, soil moisture, and hydrogen ion concentration in the soil. The variation that remains unaccounted for must be looked for in other factors, such as the impact of disturbance by man and his agents (i.e., livestock), specific ions in the soil, soil texture, experimental error, or other unmeasured factors.

Almost all of the species studied exhibited distinctive distribution patterns in relation to the total soluble salts gradient, as did some of the vegetative growth forms (i.e., shrubs, grasses, succulent stemmed species, forbs, and perennials). This would indicate that the salt gradient was important as an environmental factor in determining the distribution patterns of the individual plant species growing around the Goshen salt playa. This fact concurs with the findings of a number of earlier authors (Lambert 1940, Harris 1920, Fautin 1946, Fireman and Hayward 1952, Al-Jibury 1972).

*Sarcobatus vermiculatus* (Fig. 2M) was most frequent around the Goshen salt playa in salt concentrations ranging from 635 to 4,901 ppm. This range corresponds to the findings of various earlier authors who stated that *S. vermiculatus* was indicative of 3,600 ppm (Harris 1920) and 4,000 ppm soluble salt (Lambert 1940). Fireman and Hayward (1952) found *S. vermiculatus* indicative of higher salt concentrations in the soil than were indicated by *Atriplex confertifolia*. This does not agree with the findings of our study. Although the basic ranges of total soluble salts in the soil were similar for *Sarcobatus vermiculatus* and *Atriplex confertifolia*, the frequency of *Atriplex confertifolia* (Fig. 2o) tended to increase with increasing salts and *Sarcobatus vermiculatus* tended to decrease in frequency.

The most salt tolerant plant species which grew around the Goshen salt playa were *Salicornia pacifica*, *Salicornia rubra*, and *Allenrolfea occidentalis*, according to salt preference index numbers (Table 5). This basic conclusion is corroborated by other studies (Flowers and Evans 1965, Fautin 1946, Harris 1920). Ungar, Hogan, and McClelland (1969) found that *Salicornia rubra* grew in wet saline soils, but did best in areas of reduced salinity. This conclusion conflicts somewhat with the findings of this study. Evidence was felt to be supportive of the hypotheses of Ungar (1966) and Barbour (1970). They stated that they believed there are few, if any, obligate halophytes, but halophytes grew in highly saline areas because they did not compete well in nonsaline environments, whereas species which grow well in nonsaline areas cannot withstand high levels of salinity, thus leaving these highly saline habitats open to "halophyte" colonization.

*Distichlis spicata* was not particularly regulated by total soluble salts in this study. This species was also found to be ubiquitous in saline areas near Lincoln, Nebraska (Ungar, Hogan, and McClelland 1969). *Distichlis spicata*, in this study, exhibited little evidence of being regulated strongly by any of the three gradient factors studied. However, it did tend to decrease in average frequency at higher pH values.

*Sarcobatus vermiculatus* was most frequent in soils where the upper 18 inches exhibited 3 to 13 percent moisture. This is in general agreement with the findings of Flowers and Evans (1965). They noted that *S. vermiculatus* grew in soils with 5.9 to 6.2 percent moisture at 30 cm depth. These findings would seem to conflict with the study by Fautin (1946), in which he stated that *S. vermiculatus* required large amounts of water. However, *S. vermiculatus* is a species which has rather long taproots and therefore the moisture content of the more shallow layers of soil would not necessarily be indicative of this species' true moisture requirements.

*Allenrolfea occidentalis*, *Salicornia rubra*, *Salicornia pacifica*, and *Distichlis spicata* all exhibit moisture preference values in excess of 20 percent (Table 3). These results generally concurred with results of other studies for the same species (Flowers and Evans 1965, Ungar, Hogan, and McClelland 1969, Hansen 1975). Although these species grew best in very moist soils, as indicated by their moisture preference values, three of them had wide ranges along the moisture gradient. *Distichlis spicata*, as was mentioned earlier, exhibited little effect by soil moisture and ranged across the moisture gradient in a manner which would indicate that the moisture levels encountered by this and a number of other species at the Goshen salt playa are not limiting. The fact that the three species just mentioned exhibited such wide ranges across the moisture gradient and yet were so limited in their habitats (with the exception of *Distichlis spicata*) tends to support the hypothesis that it was competition from other species which was limiting their distribution.

Very definite responses to the hydrogen ion concentration gradient can be observed for a large number of the plant species involved in this study. Although there was a significant correlation between the soil moisture and hydrogen ion concentration gradients (Table 4), there also existed sufficiently different responses by several species (i.e., *Distichlis spicata, Salicornia pacifica, Allenrolfea occidentalis, Triglochin maritima, Sarcobatus vermiculatus, Bromus tectorum,* etc.) to indicate that hydrogen ion concentration influenced the distribution patterns of the plant species around the Goshen salt playa.

In their study of *Salicornia pacifica,* Hansen and Weber (1975) stated that *Salicornia pacifica* was found in the soils with pH values of 7.7, and that *Distichlis spicata* tolerated higher hydrogen ion concentrations than *Salicornia pacifica.* In this study, *Salicornia pacifica* was found to be almost completely restricted to soils with pH values in excess of 9.0, but *Distichlis spicata* became less frequent when soil pH values exceeded 8.70. Hansen and Weber also stated that *Distichlis spicata* may survive in soils with pH values between 8.0 and 9.0. The results of this study support the supposition of Hansen and Weber regarding the pH range of *Distichlis spicata.*

Quigley (1956) found that *Allenrolfea occidentalis* consistently occurred in soils of pH 8.0 and above. Flower and Evans (1965) indicated in their results that *A. occidentalis* was found in soils of about pH 8.4. The results of these two studies concur with the findings of our study, which indicate that *A. occidentalis* was most frequent between pH 8.32 and 8.70.

*Sarcobatus vermiculatus* (Fig. 4) was found to be most frequent in soils with pH values of about 8.50. Flower and Evans' (1965) results indicate that *S. vermiculatus* grew in soils with pH values of 8.6 to 9.6. Fireman and Hayward found that *S. vermiculatus* grew in soils with higher pH values than the soils in which *Atriplex confertifolia* grew. This agrees with the findings of Flowers and Evans (1965). In our study *Atriplex confertifolia* (Fig. 4) and *Sarcobatus vermiculatus* were most frequent in soils with pH values around 8.5, with *Atriplex confertifolia* exhibiting higher frequencies at slightly higher pH values. The hydrogen ion concentration preference values (Table 5) for these two species were 8.46 for *Sarcobatus vermiculatus* and 8.51 for *Atriplex confertifolia.*

The response of the plant growth forms to the hydrogen ion concentration gradient were, in most cases, dissimilar with respect to their responses to total soluble salts and soil moisture and tended to indicate an independent effect of pH upon the distribution of the plant species. Ungar, Hogan, and McClelland (1969), on the basis of results from their study of saline areas near Lincoln, Nebraska, stated that hydrogen ion concentration had little or nothing to do with plant distribution, but, as shown by the evidence from this study, hydrogen ion concentration was a factor in the distribution of plant species around the Goshen salt playa. This conclusion is in agreement with the findings of Fireman and Hayward (1952).

Due to the time of year that soil samples were taken, it is felt that some of the data presented in this study may be somewhat misleading. Specifically, the data pertaining to annual habit and gradient correlations may be incorrect. This is because the plant s*Bromus tectorum, Lepidium perfoliatum, Camelina microcarpa,* and *Descurainia sophia* (all spring annuals) had completed their life cycles before the time soil samples were taken. These species germinate and complete their life cycle in the spring when there exist more favorable moisture conditions in their habitats. During this time of year, the excess moisture probably leaches the soil salts downward and out of reach of the roots of these spring annuals. As the soil dries during early summer the salts are returned to the surface by the wicking action described by Hansen and Weber (1975). Thus, although the annuals did occur on some saline sites, the sites probably were far less saline while the annuals were alive and growing.

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# DISTRIBUTION OF SCULPINS IN THE CLEARWATER RIVER BASIN, IDAHO

O. Eugene Maughan[1] and Gary E. Saul[2]

Abstract.— The distributions of *Cottus bairdi*, *C. rhotheus*, and *C. beldingi* exhibited a highly significant positive degree of association. Conversely, the distribution of *C. confusus* exhibited a highly significant negative association with the distributional complex, *C. bairdi*, *C. rhotheus*, and *C. beldingi*. These species of sculpins can be grouped into two assemblages; one based on the distribution of *C. confusus* and the other based on the combined distributions of the other three species. The factor or factors limiting the downstream distribution of *C. confusus* or the upstream distribution of the other three species could not be positively identified. However, we hypothesize that competition between *C. confusus* and one or more members of the *C. bairdi*, *C. rhotheus* and *C. beldingi* complex is involved. In the area of overlapping distributions among *C. bairdi*, *C. rhotheus*, and *C. bairdi* we hypothesize that resource partitioning is occurring. However, the data did not allow evaluation of this hypothesis.

Species that are closely related and morphologically similar are often assumed to compete. It is further often assumed that simultaneous occurrence at a given location indicates little or no competition, whereas exclusion from a site indicates intense competition. Although this hypothesis is largely untested, the coordinated or contiguous distributions of closely related species suggests the opportunity to gain insight into species interactions where such a phenomenon occurs.

Competitive interaction between species of the same genus *Cottus* is probable, and information on the distribution of several species over a large area is available (Maughan 1976). The objective of this paper is to assess the degree of contiguity in the distribution of four species of sculpins from the Clearwater drainage in north central Idaho as a clue to the intensity of interspecific interactions.

## Materials and Methods

Fish were collected from 114 locations from June to September in 1969 and 1970. Collection sites were approximately 10 miles apart, and collections were made using a small Y net (Bond 1963) or a 6-ft seine in conjunction with a backpack electroshocker. In the Selway Bitterroot Wilderness area, only a seine was used. Fish were preserved in 10 percent formalin, and later transferred to 70 percent alcohol.

Repetitive Chi-square tests for species association (Kershaw 1971) were conducted between individual species and various species complexes in an attempt to elucidate the associative distributions of *C. bairdi*, *C. rhotheus*, *C. beldingi*, and *C. confusus*.

## Results

The distributions of *C. bairdi* and *C. rhotheus* exhibited a highly significant positive degree of association (Table 1). These two species occurred together in 68 percent of all samples in which either species was taken. Likewise, the distribution of *C. beldingi* demonstrated a highly significant positive association with the distributional complex of *C. bairdi* and *C. rhotheus* (Table 1). *Cottus beldingi* occurred in 92 percent of all

Table 1. Chi-square values for tests of species association of four species of cottids from the Clearwater River drainage 1969–70.

| Species comparisons | $X^2$ | df |
|---|---|---|
| *C. bairdi* vs. *C. rhotheus* | 49** | 1 |
| *C. beldingi* vs. *C. bairdi*, *C. rhotheus* | 44** | 3 |
| *C. confusus* vs. *c. beldingi*, *C. bairdi*, *C. rhotheus* | 19.25** | 7 |

**(P<0.01)

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collections in which either *C. bairdi* or *C. rhotheus* was taken and in addition appeared in 30.8 percent of all collections in which neither *C. bairdi* nor *C. rhotheus* was taken (Table 2, Fig. 1).

The distribution of *C. confusus* exhibited a highly significant negative association with the distributional complex of *C. bairdi*, *C. rhotheus*, and *C. beldingi* (Table 1). *Cottus confusus* appeared in only 13 percent of all collections in which either *C. bairdi* or *C. rhotheus* or *C. beldingi* was taken, but was present in 42.2 percent of all samples in which none of the other three species occurred (Table 3, Fig. 2).

Table 2. Distributional frequency of occurrence of *C. beldingi* and the complex of *C. bairdi* and *C. rhotheus*.[*]

| | | *C. bairdi* and *C. rhotheus* | | |
|---|---|---|---|---|
| | | $^{+}1^{+}2$[**] | $^{+}1^{-}1\cdot{}^{-}1^{+}2$ | $^{-}1^{-}2$ |
| *C. beldingi* | + | 30 | 15 | 20 |
| | – | 1 | 3 | 45 |

[*] The Chi-square contingency table presented is a modified form of the 2×4 contingency table utilized in the analysis of *C. beldingi* vs. *C. bairdi* and *C. rhotheus*. The combinations of either *C. bairdi* or *C. rhotheus* occurring while the other was absent were collapsed into one cell for illustrative purposes.

[**] Subscripts of 1, 2 correspond to *C. bairdi* and *C. rhotheus*, respectively.

+ = presence – = absence

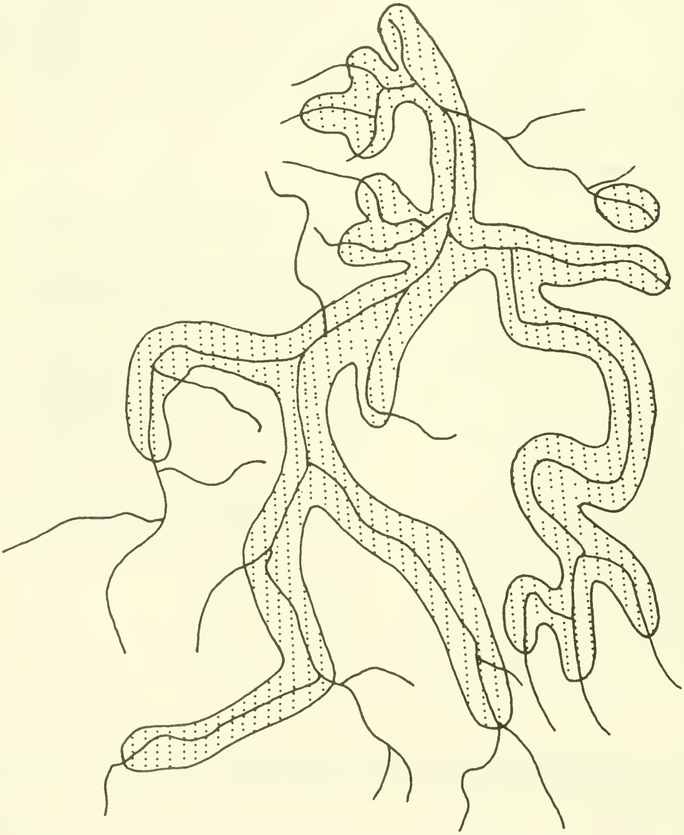

Fig. 1. Area of the Clearwater River basin occupied by one or more of the species *C. beldingi*, *C. bairdi*, and *C. rhotheus*.

TABLE 3. Distributional frequency of occurrence of *C. confusus* and the complex of *C. bairdi*, *C. rhotheus*, and *C. beldingi*.[*]

| | | ${}^{+}1{}^{+}2{}^{+}3$[**] | ${}^{+}1{}^{+}2{}^{-}3$,...<br>${}^{-}1{}^{+}2{}^{+}3$ | ${}^{-}1{}^{-}2{}^{-}3$ |
|---|---|---|---|---|
| *C. confusus* | + | 2 | 7 | 19 |
| | – | 28 | 32 | 26 |
| | | *C. bairdi*, *C. rhotheus*, and *C. beldingi* | | |

[*] The Chi-square contingency table presented is a modified form of the $2 \times 8$ contingency table utilized in the Chi-square analysis of *C. confusus* vs. *C. bairdi*, *C. Rhotheus*, *C. beldingi*. All possible combinations of *C. bairdi*, *C. rhotheus*, and *C. beldingi* (except all present or all absent) have been collapsed into one cell.

[**] Subscripts of 1, 2, 3 = *C. bairdi*, *C. rhotheus*, and *C. beldingi*, respectively.

+ = presence – = absence

## DISCUSSION

The findings of this study indicate that species of sculpins in the Clearwater system can be grouped into two major assemblages based on the distribution of *C. confusus* vs. the distribution of the *C. rhotheus*, *C. bairdi*, and *C. beldingi* complex. The data did not allow identification of the factor or factors limiting each species group. However, C. rhotheus, C. bairdi, and *C. beldingi* would appear to be generally responding to the same factor or factors. We believe that partitioning of resources is probable among *C. bairdi*, *C. rhotheus*, and *C. beldingi* in areas of coexistence, and that extreme competition occurs between that complex and *C. confusus* ($X^2$

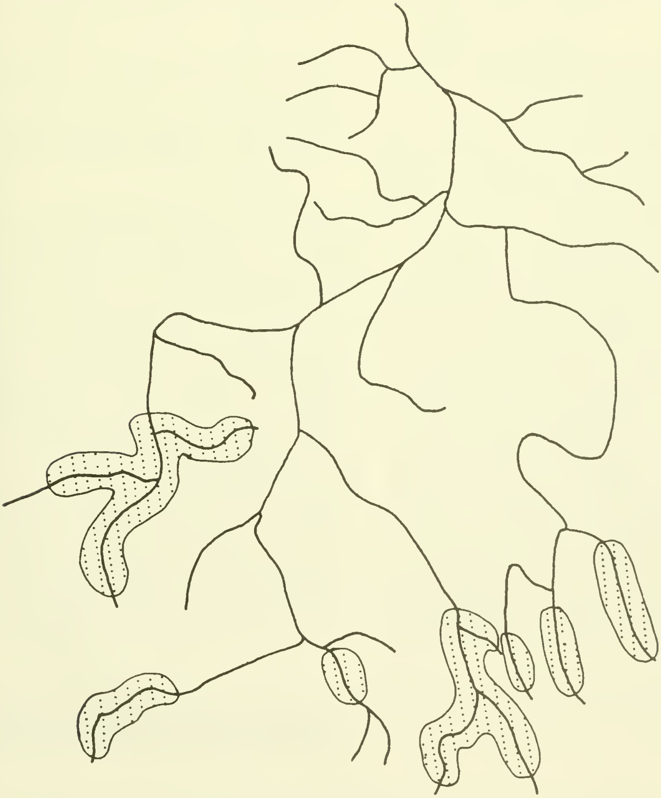

Fig. 2. Area of Clearwater River basin occupied by *C. confusus*.

19.25**). This competition is responsible for the exclusion of *C. confusus* from areas occupied by one or more of the other species.

Repetitive analyses on the same data (i.e., testing several nonindependent hypotheses with the same data) increase the probability of exposing a significant result on the basis of chance alone (Type I Error) and increase the alpha level an undetermined amount. However, the highly significant Chi-squares encountered in these analyses (e.g., $X_1^2 = 49$) make it extremely unlikely that these results could be contributed by chance alone, even with an inflated alpha level.

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# PHYTOSEIID PREDATORS OF MITE PESTS IN UTAH APPLE ORCHARDS[1]

Clive D. Jorgensen[2] and Vichitra Mongkolprasith[2,3]

Abstract.— Recent efforts to integrate phytoseiid predators in pest (mite) management programs for apples have been somewhat successful and economical in several fruit growing areas of North America. Convenient descriptions and reviews of the literature for species which have been collected from Utah are provided to stimulate further local work. Seven species of *Amblyseius* and five *Typhlodromus* are described (none new), with notes provided concerning their respective geographic distributions and biologies.

Chemical control of phytophagous mites in apple orchards has resulted in pesticide residues toxic to man, death of nontarget species in the agro-ecosystem, inflated expenses, polluted environments, and the development of resistance to numerous pesticides by the pests themselves. The avoid these problems, some pest management programs now include biological agents (predators, parasites, pathogens). Among these agents, phytoseiid predators have received attention because of their numbers, common occurrence with the pests, and important role demonstrated in economically suppressing some pest mite species while avoiding pollution and toxic residues.

Before integrating phytoseiid predators into pest control programs, taxonomic studies should be made to determine the species present and their potentials for pest control. Although phytoseiid mites were studied from an economic standpoint by Parrott et al. (1906), reliable taxonomic identifications were not possible until 1948 when Garman used chaetotaxy of the dorsal and ventrianal shields in his generic revision. Nesbitt (1951) later revised the subfamily using Garman's system of chaetotaxy and suggested several species as important predators of tetranychid mites. Chant (1959) started a series of papers dealing with phytoseiid biology that has led to many useful faunistic and life history studies, i.e., Muma (1961), Pritchard and Baker (1962), Schuster and Pritchard (1963), Chant (1965), Chant and Hansell (1971), Chant et al. (1974), Oatman (1976), etc. A recent review of the literature (Croft and Brown 1975) was helpful in understanding potential success of phytoseiid predators in pest management of deciduous fruit pests. Additional information has since been prepared by Croft (1975a, 1975b) in summaries of the US/IBP pome and stone fruit pest management research and strategies.

Although phytophagous species have been listed by Jorgensen (1967) for Utah apple orchards, few studies of potential predators have been completed. Except for important life history studies of *Typhlodromus mcgregori* (Croft and Jorgensen, 1969) and *Typhlodromus occidentalis* (Lee and Davis, 1968), little is known of Utah species, and faunal studies have not even been reported.

Descriptions of Utah phytoseiid species on apples are presented below, along with a key for identifying adult females. Classification of the species and genera follows Chant (1965), Chant and Hansell (1971), and Chant et al. (1974). The terminology and chaetotaxy follow Schuster and Pritchard (1963). Seasonal variations and distributions within the trees are not present because they are found for several species in Leetham and Jorgensen (1969), Nelson and Jorgensen (1969), and Duke et al. (1970). The primary objectives of our study are (1) to provide a basis for identifying the predaceous mites that are potentially helpful in pest management of Utah apple orchards and (2) to summarize what is presently known of their respective biologies.

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[1] This research was supported, in part, by Grant 12-14-100-3029-(33) from the USDA, Division of Entomology, to Brigham Young University.

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## METHODS

Specimens were collected from derelict and commercial apple orchards throughout the state. The collections were made from all geographic regions and included sampling from leaves, bark from the trunk and major scaffold limbs, and orchard cover and litter from beneath the trees. A mite-brushing machine was sometimes used to collect mites from leaves and twigs. Modified Tullgren funnels were used extensively to remove mites from cover and litter as well as from twigs and leaves, particularly during the winter months. Collections were started in 1966 and continued through 1973, although most collections were made from 1966 to 1971.

Specimens were mounted in Hoyers medium, identified, and drawings made of them with the assistance of a drawing tube. Measurements were taken from intact specimens and routinely checked for accuracy by remeasuring. Although we did not think it was necessary to report complete descriptions and measurements, they are available in Mongkolprasith (1976). Complete descriptions are also referenced with each species discussion.

Nomenclature used for chaetotaxy throughout this paper is included in Figures 1 and 2. Although the lateral setae (laterals) are labeled prolateral and postlateral (Fig. 1), they are numbered sequentially $L_{1-9}$ in the descriptions; thus (Fig. 1) prolaterals = $L_{1-6}$, postlaterals = $L_{7-9}$, dorsocentrals = $D_{2-5}$, verticals = $D_1$ and clunals = $D_6$.

## RESULTS

### Key to the Adult Females[4]

1. Four pairs of prolateral setae on the dorsal plate; never more than a total of nine pairs of lateral setae (Figs. 4–17); genus *Amblyseius* .......... 2

— More than four pairs of prolateral setae on the dorsal plate; 8–12 pairs of lateral setae (Figs. 1, 18–27); genus *Typhlodromus* .......... 8

2(1). All setae on the dorsal plate short or minute, none greatly (at least twice as long) longer than the others (Figs. 4, 5) .......... *A. salish*

— At least one pair of setae on the dorsal plate ($L_1$, $L_4$, $L_9$, or $M_2$) twice as long as other setae .......... 3

3(2). Prolateral setae longer than distances between their bases, $L_5$ extends beyond the bases of $L_6$ (Figs. 6, 7) .......... *A. fallacis*

— Prolateral setae shorter than the distances between their bases, $L_5$ not long enough to reach the base of $L_6$ .......... 4

4(3). Only $L_9$ at least twice as long as other setae on the dorsal plate (Figs. 8, 9) .......... *A. cucumeris*

— More than one pair of setae (usually $L_1$, $L_4$, $L_9$, or $M_2$) on the dorsal plate at least twice as long as others .......... 5

5(4). $D_5$ present on the dorsal plate (Figs. 10, 11) *A. floridanus*..........

— $D_5$ absent from the dorsal plate .......... 6

6(5). $L_9$ longer than $M_2$, preanal pores behind and almost in line longitudinally with the third preanal setae (Figs. 12, 13) .......... *A. oregonensis*

— $L_9$ slightly shorter than $M_2$, preanal pores nearly in line with or slightly in front of the third preanal setae .......... 7

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[4] Complete descriptions of each species are cited on the first line under each species heading in this section. For measurements and descriptions of Utah specimens, refer to Mongkolprasith (1976).

7(6). Length of $L_2$ about two-thirds of $L_1$ $M_2$ and $L_9$ slightly serrate; macroseta on basitarsus IV longest, shortest on tibia (Figs. 3, 14, 15) .............................. *A. rosellus*

— Length of $L_2$ about five-sixths of $L_1$ $M_2$ and $L_9$ smooth. Macroseta on basitarsus IV longest, approximately equal on tibia and genu (Figs. 3, 16, 17) .......... *A. ovatus*

8(7). Eight pairs of lateral setae on the dorsal plate .................................................................. 9

— More than eight pairs of lateral setae on the dorsal plate .......................................... 10

9(8). Two pairs of preanal setae on the ventrianal plate (Figs. 18, 19) .................. *T. smithii*

— Four pairs of preanal setae on the ventrianal plate (Figs. 20, 21). ................................................................................................................ *T. columbiensis*

10(8). Ten pairs of lateral setae on the dorsal plate (Figs. 22, 23) ...................... *T. caudiglans*

— Nine pairs of lateral setae on the dorsal plate ........................................................... 11

11(10). $L_9$ at least twice as long as $L_8$, prolateral setae equal to or slightly longer than the distances between their bases and succeeding setae (Figs. 24, 25). ............................................................................................................... *T. mcgregori*

— $L_9$ approximately equal in length to $L_8$, lateral setae much longer than the distances between their bases and succeeding setae (Figs. 26, 27) ......... *T. occidentalis*

### *Amblyseius salish* Chant & Hansell

Fig. 4, 5

Chant and Hansell, 1971:717, Figs. 97–100, 218

Dorsal plate nearly oval, about twice as long as wide, smooth. Dorsal setae smooth, minute, shorter than distances between their bases and bases of nearest succeeding neighbors. Lateral setae longer than dorsals and increase generally in length posteriorly, but always shorter than distance to the base of the nearest succeeding setae. Two pairs of pores and $M_2$ closer to $L_7$ than $L_8$. Sublaterals $S_1$ and $S_2$ present. Peritremes extend to the base of vertical setae.

Utah specimens agree with data provided by Chant and Hansell (1971) for specimens collected from Canada and Alaska. *Amblyseius salish* has been reported only from Ontario and northwest British Columbia (Chant and Hansell 1971). Utah specimens were collected from bark and leaves of apple trees, and cover and litter from apple orchards in Utah County.

### *Amblyseius fallacis* (Garman)

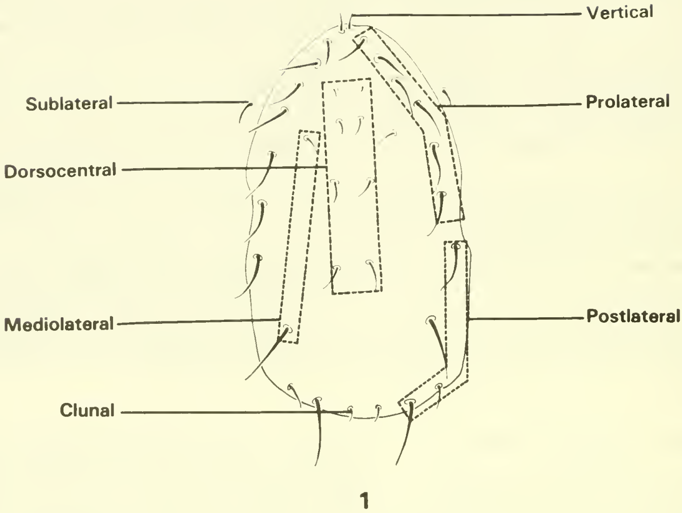
Fig. 6, 7

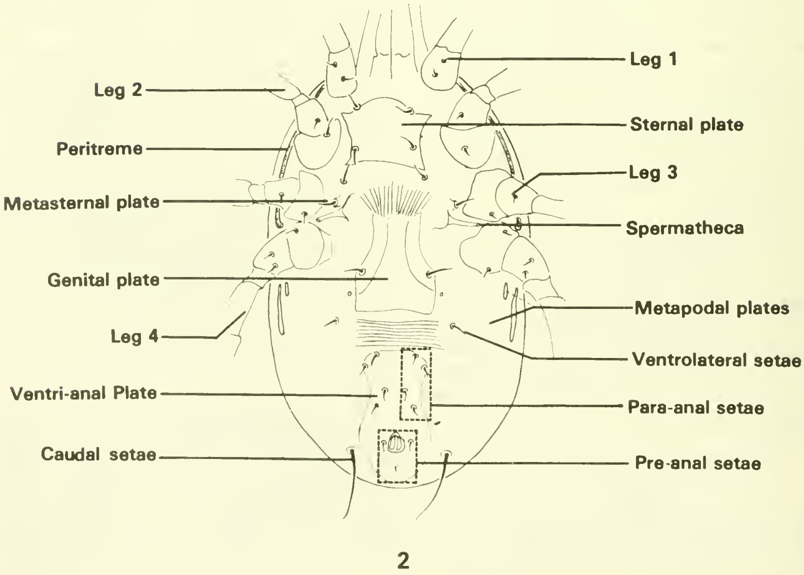
Chant and Hansell, 1971:707, Figs. 8–12, 227

Dorsal plate reticulate and nearly twice as long as wide. Dorsal setae, except $D_6$, long and slender, but usually not longer than distances between their bases and the bases of nearest succeeding neighbors. Lateral setae except $L_4$, longer than distances between their bases. Sublaterals $S_1$ and $S_2$ present. Postscutum with four pairs of pores. Peritremes large and long, extending midway between $L_1$ and verticals in females and well beyond $L_1$ in males.

*Amblyseius fallacis* has been separated by previous authors from closely related species as follows: (1) lengths of setae on the dorsal hexagonal area were used to distinguish it from *A. masseei* (Chant 1965, 1957, 1959, and Womersley 1954); (2) relative lengths of $D_2$ and $D_3$, distances between their bases (Chant and Hansell 1971); and (3) number and shape of postscutum and preanal pores were used (Garman 1948 and Schuster and Pritchard 1963) to distinguish it from *A. inornatus*. Utah specimens have $D_2$ and $D_3$ longer or equal to the crescentic preanal pores; thus they were determined to be *A. fallacis*.

This species has been reported from throughout North America, parts of Australia (Womersley 1954), and Algeria (Ehara 1966). In Canada, it has been reported from British Columbia (Chant 1957, Anderson et al. 1958a) and eastern Canada (Nesbitt 1951, Chant and Hansell 1971). Specimens have been reported in the United States from Connecticut (Garman 1948), New York (Nesbitt 1951), Virginia (Nesbitt 1951), Washington


Vertical
Sublateral
Prolateral
Dorsocentral
Postlateral
Mediolateral
Clunal
1


Leg 1
Leg 2
Sternal plate
Peritreme
Leg 3
Metasternal plate
Spermatheca
Genital plate
Metapodal plates
Leg 4
Ventrolateral setae
Ventri-anal Plate
Para-anal setae
Caudal setae
Pre-anal setae
2

Figs. 1–2. Labeled dorsal (1) and ventral (2) views of *Typhlodromus mcgregori*.

(Nesbitt 1951, Malcolm 1955, Burrell and McCormick 1964), West Virginia (Clancy and McAlister 1958), Wisconsin (Oatman 1965), Ohio (Ballard 1954, Ristich 1956), Maryland (Smith et al. 1963), Illinois (English and Snetsinger 1957), Texas (Dean 1957), California (Schuster and Pritchard 1963) and Utah (Leetham and Jorgensen 1969). Cunliffe and Baker (1953) reported specimens from across the entire northern part of the United States. We collected them from apple leaves and spurs, and apple tree cover from Utah, Wasatch, and Duchesne counties in Utah.

Considerable work has been done on the life history, host species and overwintering of *A. fallacis* (Ballard 1954, Smith and Newsom 1970, Tsung 1972). They have been reported to feed on *Tetranychus telarius*, *Tetranychus canadensis*, *Schoenei mcgregori*, and *Panonychus ulmi* (Nesbitt 1951); *Tetranychus urticae*, *Tetranychus mcdanieli*, *P. ulmi*, and *Bryobia* sp. (Herbert 1959, Burrell and McCormick 1964); and *Tetranychus yusti*, *Tetranychus desertorum*, and *T. urticae* (Smith and Newsom 1970). They have been reported from apple (Garman 1948), peach (Putman and Herne 1964), apple, raspberry, strawberry, bean, corn, dogbane, and clover (Nesbitt 1951); sugar beets, alfalfa, and morning glory (Burrell and McCormick 1964); and asparagus (Tsung 1972). Specimens have been reported overwintering on apple spurs (Leetham and Jorgensen 1969, Tusing 1972) and orchard litter and cover (Putman 1959).

Although Chant (1961) considered *A. fallacis* an unlikely control agent of *T. telarius* in greenhouses, Smith and Newsom (1970) recognized their potential as being rather high for several tetranychid species. They have recently been found to be rather effective in controlling tetranychid species in Michigan and other U.S. apple growing areas east of the Mississippi where they have developed resistance to organic phosphate insecticides (Croft 1975a, 1975c).

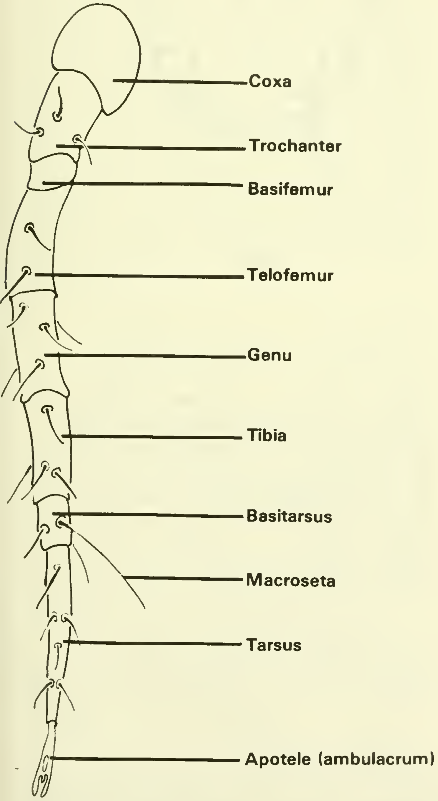


Fig. 3. Labeled leg IV of *Typhlodromus columbiensis*.

### *Amblyseius cucumeris* (Oudemans)

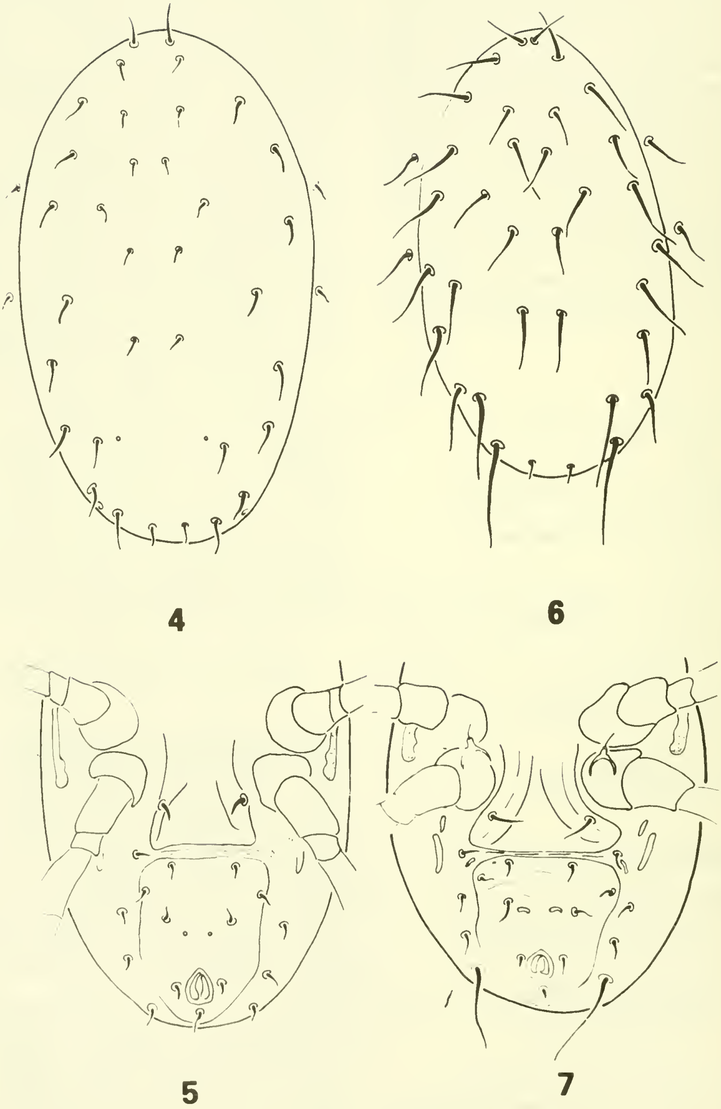
Figs. 8, 9

Chant and Hansell, 1971:721, Figs. 129–132, 210

Dorsal plate reticulate, oval, slightly imbricated. Dorsal setae generally smooth and short, all being shorter than distances between their bases and bases of nearest succeeding neighbors, except $L_8$ longer than intersectional distance between $L_8$ and $L_9$. Prolateral setae shortened, approximately equal in length, sublaterals $S_1$ and $S_2$ present. Peritremes extend nearly to base of vertical setae and slightly shorter in males than in females.

Although the Utah specimens fail to satisfy the distinguishing characters described by Chant (1957, 1959) and DeLeon (1959), they agree with Wormersley (1954), Schuster and Gonzales (1963), Schuster and Pritchard (1963), and Chant and Hansell (1971).

This species seems to be found throughout the world, being reported from British Co-



Figs. 4–7. Dorsal (4) and ventral (5) views of *Amblyseius salish*, and dorsal (6) and ventral (7) views of *Amblyseius fallacis*.

lumbia, Canada (Chant 1957, Anderson et al. 1958); eastern Canada (Nesbit 1951); England (Collyer 1956); Switzerland, Germany, Netherlands, New Zealand, Mexico, Egypt, Australia (Chant 1959); Algeria (Ehara 1966); and in the United States, Virginia (Collyer 1956), California (Schuster and Pritchard 1963), and Utah (Leetham and Jorgensen 1969). They were collected from apple leaves and bark and apple orchard litter and cover in Utah and Salt Lake counties in Utah.

Life history studies have not been extensive, although considerable work has been reported (Oudemans 1930, MacGill 1939, El-Badry and Zaher 1961). They have been reported feeding on *Steneotarsonemus paplidus* (Huffaker and Kennett 1956), *Panonychus ulmi* and *Bryobia* sp. (Burrell and McCormick 1964), and *Tetranychus cinnabarinus, Eutetranychus banksi, Oligonychus terminalis,* and *Brevipalpus* sp. (El-Badry and Zaher 1961). Host plants from which they have been collected are beans, dogbane (Nesbitt 1951); cotton (MacGill 1939), tomatoes (Evans 1952); myrobalam, bramble, strawberry (Collyer 1956); peach (Putman 1959); eggplant, ornamentals, several fruit trees (El-Badry and Zaher 1961); and violets, sugar beets, and white sage (Burrell and McCormick 1964).

### *Amblyseius floridanus* (Muma)

Figs. 10, 11

Schuster and Pritchard, 1963:234, Fig. 24

Dorsal plate oval, smooth, broadest behind legs IV. Dorsal setae smooth, minute except $D_1$ longer than others. Prolateral setae (except $L_1$) shorter than distances from their bases and bases of nearest succeeding neighbors. Dorsal setae $M_2$, $L_1$, $L_4$, and $L_9$ much longer than other setae. Sublaterals $S_2$ slightly shorter than $S_1$. Peritremes extend slightly beyond $L_1$.

Muma (1955) stated that *A. floridanus* has no preanal pores, but the Utah specimen agrees with descriptions by Garman (1958), Schuster, and Pritchard (1963), and Muma (1964).

This species has been reported from Hong Kong and Algeria (Ehara 1966), and, in the United States, from Florida (Garman 1948, Muma 1955), California, Oregon, Washington, and New Mexico (Schuster and Smith 1960, Schuster and Pritchard 1963), and Utah (Leetham and Jorgensen 1969). In Utah, *A. floridanus* was collected from Utah and Cache counties on apple leaves and in the litter and cover of apple orchards. Biological research has apparently not yet been done.

### *Amblyseius oregonensis* (Garman)

Fig. 12, 13

Chant 1959:91, Figs. 196–197

Dorsal plate smooth, oval. Dorsal setae smooth, minute, with $D_5$ missing, always shorter than distances from their bases to bases of nearest succeeding neighbors. Lateral setae longer than dorsals, $L_4$, $L_9$, and $M_2$ much longer than other laterals with $L_9$ at least twice as long as others. Two pairs of pores. Sublaterals $S_1$ and $S_2$ present. Peritremes extend to bases of vertical setae.

Although some Utah specimens resemble descriptions of *Amblyseius rosellus* reported by Chant and Baker (1965), they agree specifically with descriptions for *A. oregonensis* in Garman (1958) and Chant (1959).

*Amblyseius oregonensis* has been reported from Washington and Connecticut (Garman 1948). In Utah, they have been collected from apple leaves and bark from Utah and Cache counties, and cover, litter, and soil in Utah County. Biological research with this species has apparently not yet been done.

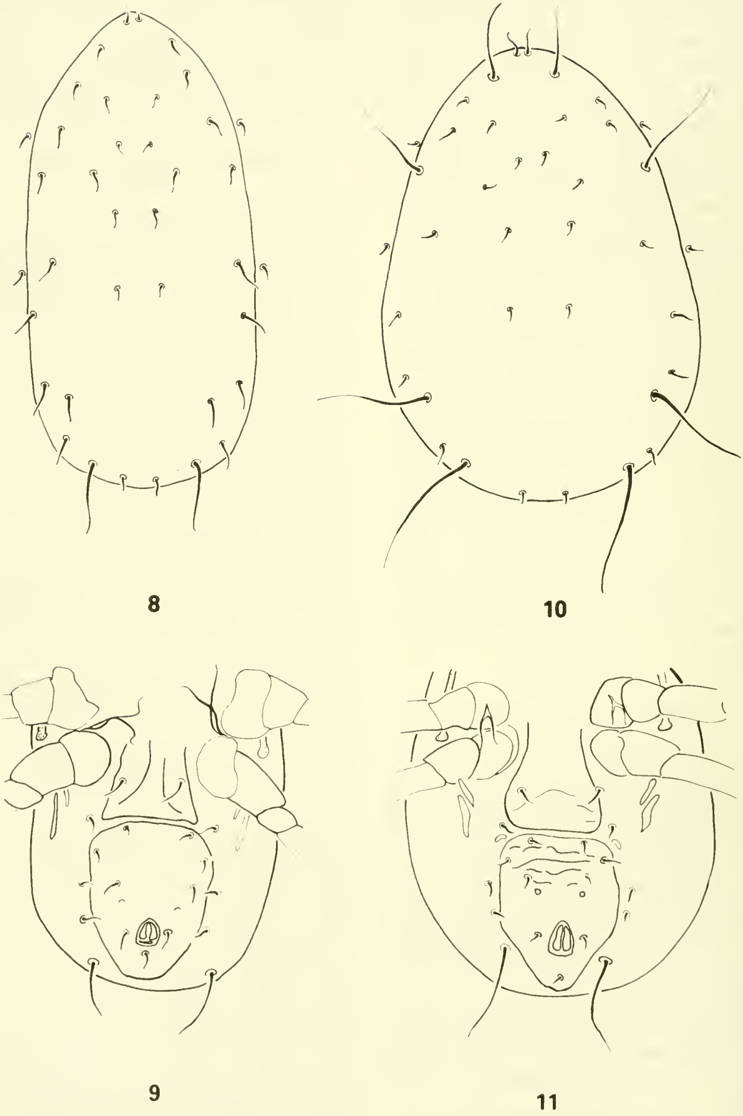
### *Amblyseius rosellus* (Chant)

Figs. 14, 15

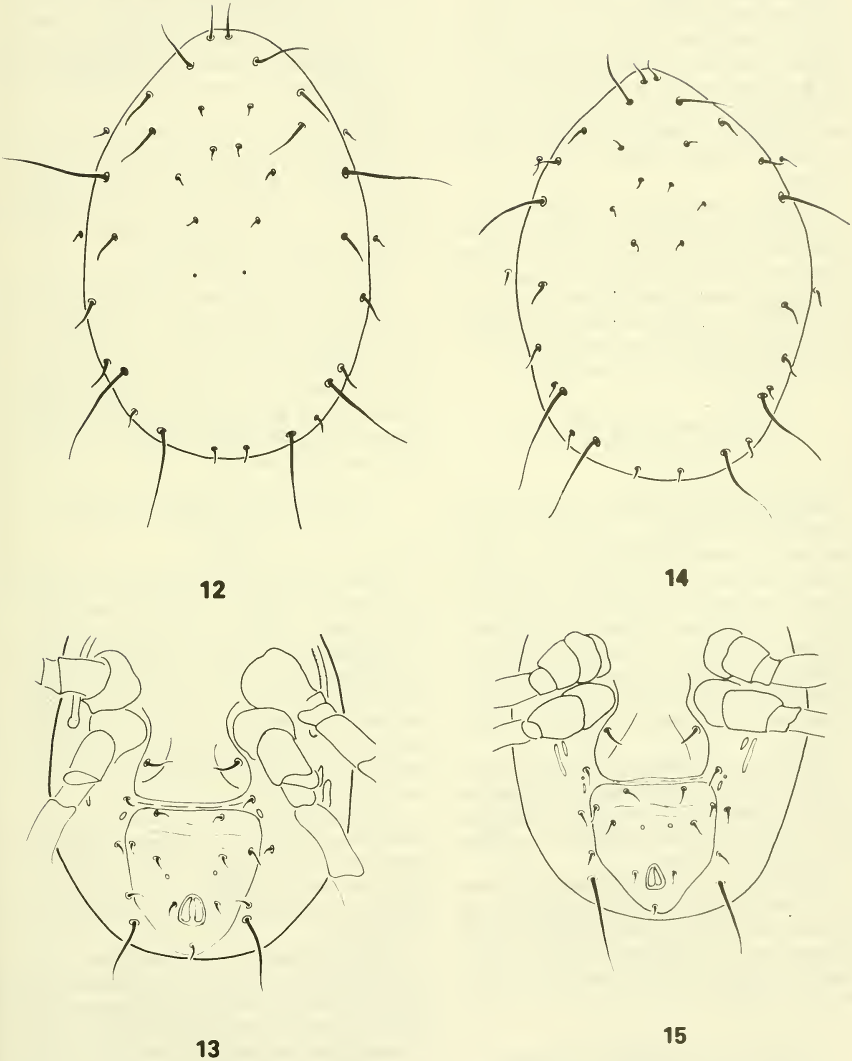
Chant and Baker, 1965:18, Figs. 94–98

Dorsal plate oval, usually smooth, sometimes slightly reticulated near margins. Dorsal setae smooth, minute, always shorter than distances from their bases to bases of nearest succeeding neighbors. Lateral setae unequal in length; $M_2$, $L_4$, and $L_9$ much longer than other setae. Sublaterals $S_1$ and $S_2$ present. Dorsal plate with two pairs of pores. Peritremes extend to bases of vertical setae.

This species has been reported from the West Indies (Chant 1959) and Mexico and Central America (Chant and Baker 1965). Specimens have been collected only from apple orchard cover in Utah County, Utah. Biological research with this species has apparently not yet been done.



Figs. 8–11. Dorsal (8) and ventral (9) views of *Amblyseius cucumeris*, and dorsal (10) and ventral (11) views of *Amblyseius floridanus*.



Figs. 12–15. Dorsal (12) and ventral (13) views of *Amblyseius oregonensis,* and dorsal (14) and ventral (15) views of *Amblyseius rosellus.*

### *Amblyseius ovatus* (Garman)

Figs. 16, 17

Schuster and Pritchard, 1963:246, Fig. 33

Dorsal plate smooth, about two-thirds as wide as long. Dorsal setae smooth, minute, always shorter than distances from their bases to bases of nearest succeeding neighbors. Lateral setae unequal in length; $M_2$, $L_4$, and $L_9$ much longer than other setae. Sublaterals $S_1$ and $S_2$ present. Dorsal shield with two pairs of pores. Peritremes extend to bases of vertical setae.

*Amblyseius ovatus* has been reported from Equador and Central America (Garman 1948, Chant and Baker 1965), and in the United States from Texas, Florida (Garman 1948, Chant and Baker 1965), Missouri (Poe and Enns 1969), and Utah (Leetham and Jorgensen 1969). Biological research with this species has apparently not yet been done.

### *Typhlodromus smithii* (Schuster)

Figs. 18, 19

Schuster, 1975:203, Figs. a–g

Dorsal plate oval, slightly to distinctly reticulate from anterior to posterior. Dorsal setae short, slender, always equal to or shorter than distances from their bases to bases of nearest succeeding neighbors. Prolateral setae on dorsal plate shorter than distances between their bases. Sublateral $S_1$ equal in length to its associated lateral seta; $S_2$ slightly longer than its associated lateral seta. Peritremes moderately long, extending to middle of coxa II.

Schuster and Pritchard (1963) revised Schuster's (1957) description and reduced the peritreme length to $S_1$. Specimens from Utah agree with the original description, extending the peritremes to coxa II.

This species has been reported from western North America by Schuster (1957) and Schuster and Smith (1960). In Utah, it was collected only from apple tree bark in Utah County. Biological research with this species has apparently not yet been done.

### *Typhlodromus columbiensis* (Chant)

Figs. 20, 21

Chant et al., 1974:1271, Figs. 19–21

Dorsal plate reticulate, slightly ridged, especially at posterior end. Dorsal setae smooth, shorter than distances from their bases to bases of nearest succeeding neighbors, increasing in length posteriorly, except $D_1$ and $D_6$. $S_1$ slightly posterior to $L_4$ and $S_2$ closer to $L_6$ than to $L_7$. Peritremes narrow and extending to vertical setae in females and one-half distance between vertical setae and $L_1$ in males.

Descriptions of Utah specimens agree with the diagnostic characters provided by Chant et al. (1974), and Muma (1961), and, although $M_2$ fails to exceed the distance between its base and $L_7$ as described by Chant (1959), they are clearly *T. columbiensis*.

Until this species was reported from Utah by Leetham and Jorgensen (1969) they were known only from British Columbia and Alaska (Chant 1959, Chant et al. 1974). Specimens from Utah were collected from apple bark and leaves from Utah, Cache, and Davis counties; and from apple orchard cover in Utah County. Biological research has apparently not yet been done.

### *Typhlodromus caudiglans* (Schuster)

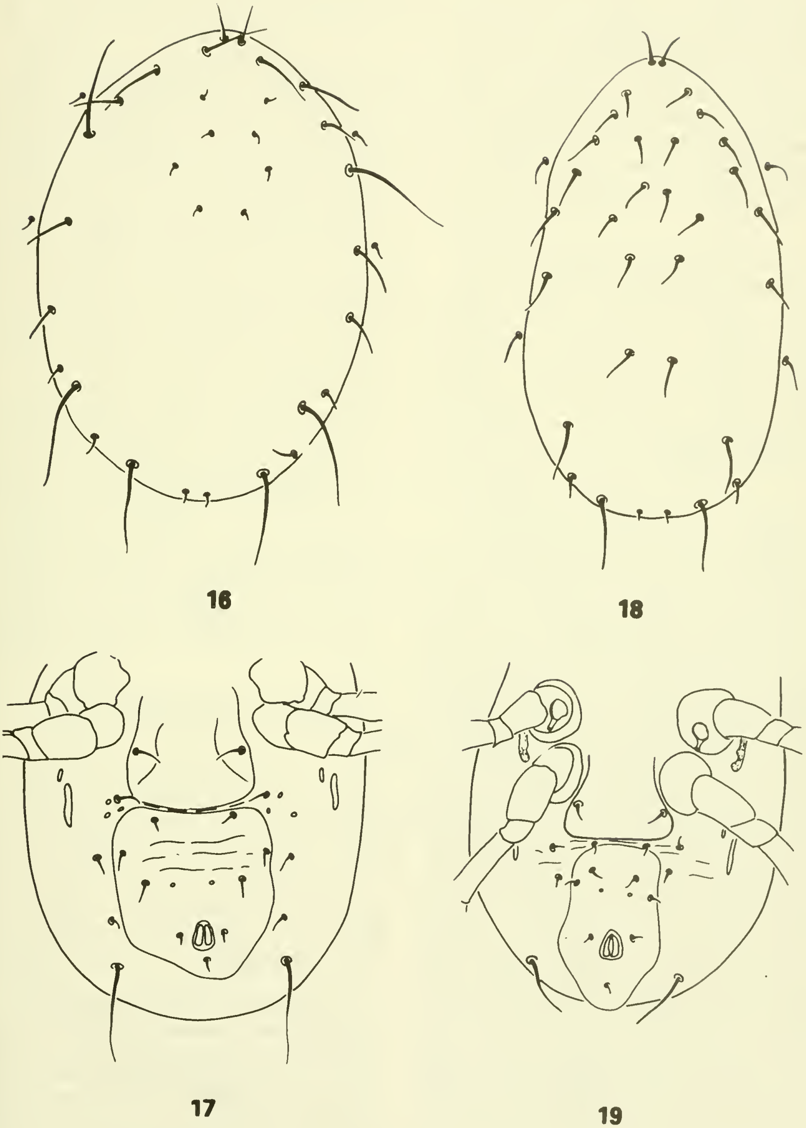
Figs. 22, 23

Chant et al. 1974:1288, Figs. 80–83

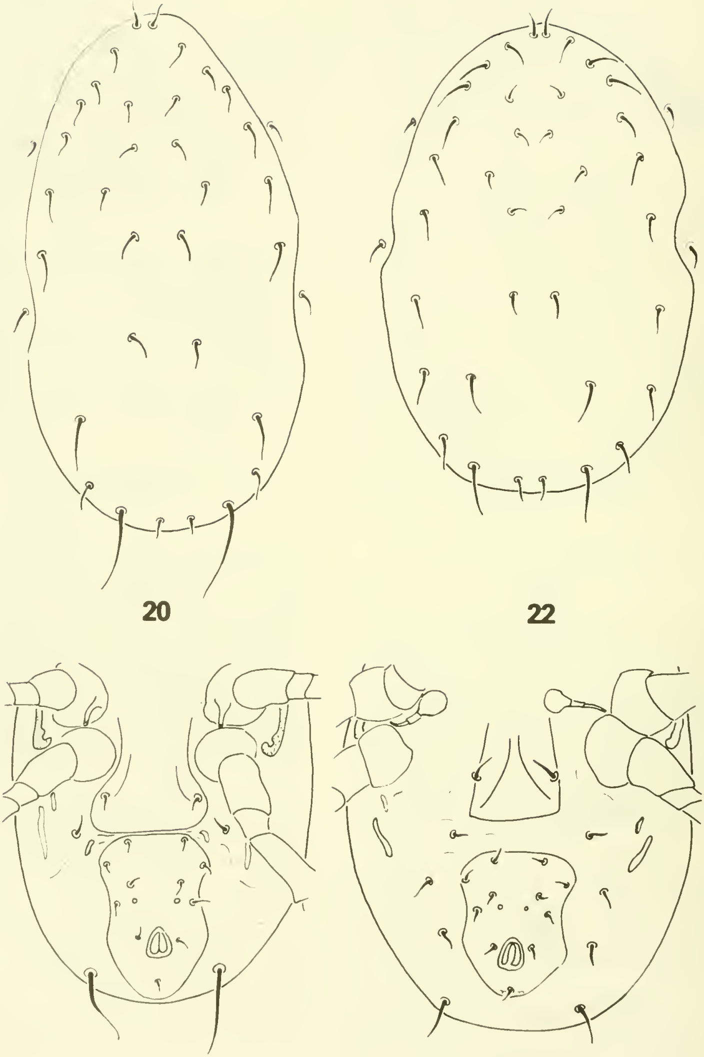
Dorsal plate about one-third longer than wide, lateral margins somewhat concave, surface appears imbricated. Dorsal setae short, slender, all but $L_9$ shorter than distances between bases of nearest succeeding neighbors. Prolateral setae on dorsal shield shorter than distances between their bases. Sublaterals $S_1$ and $S_2$ present and equal in length. Peritremes extend slightly beyond $L_1$ setae but not to vertical setae.

Although the Utah specimens possess macrosetae on leg IV that Chant (1959) and Schuster (1959) failed to observe, they conform to the redescriptions submitted by Schuster and Pritchard (1963) and Chant et al. (1974).

This species has been reported from Egypt (El Badry and Zaher 1961), New Zealand and England (Collyer 1964) and throughout Canada (Chant et al. 1974). In the United States *T. caudiglans* has been reported from California (Chant 1959, Schuster 1959, Schuster and Pritchard 1963, Chant et al. 1974), Wisconsin (Oatman 1960), western North America (Schuster and Smith 1969), and Utah (Lee-



Figs. 16–19. Dorsal (16) and ventral (17) views of *Amblyseius ovatus*, and dorsal (18) and ventral (19) views of *Typhlodromus smithii*.



20

22

21

23

Figs. 20–23. Dorsal (20) and ventral (21) views of *Typhlodromus columbiensis*, and dorsal (22) and ventral (23) views of *Typhlodromus caudiglans*.

tham and Jorgensen 1969). In Utah, specimens were collected from apple leaves and spurs in Utah, Cache, and Duchesne counties.

Life history studies have been provided by Schuster (1959) and Putman (1962). Putman (1962) found them able to reproduce on pollen and fungal spores, but not on *Tetranychus telarius* eggs. They have also been reported feeding on *Panonychus ulmi* and *Panonychus citri* (McMurtry and Scriven 1964) active stages, *Bryobia arborea* and *Aculus cornutus* (Putman 1962). Although specimens are found on leaves (Putman and Herne 1964), they seem to move freely from bark and spurs to leaves and back again (Putman 1962, Putman and Herne 1964). The variety of "host" trees also seems to influence movement and relative abundance. Putman (1962) and Putman and Herne (1964) found greater movement on peach than apple, and Downing and Moilliet (1967) found them more numerous on Spartan and McIntosh apple varieties than on Delicious.

Generally, because of feeding habits and habitat selection, *T. caudiglans* cannot be considered a good prospect in integrated pest management programs. Clearly, more research is required to demonstrate positive considerations.

### *Typhlodromus mcgregori* (Chant)
Figs. 24, 25

Chant et al., 1974:1281, Figs. 54–57

Dorsal plate slightly reticulate, stippled with small punctuations over its entire surface. Dorsal setae short, usually shorter than distances from their bases to bases of nearest succeeding neighbors. Prolateral setae on dorsal plate long, extending to and slightly beyond bases of succeeding setae. Sublateral $S_2$ absent. Peritremes extend to bases of vertical setae.

The character used by Chant (1959), Chant et al. (1974), and Schuster and Pritchard (1963) to separate *T. mcgregori* from *T. flumenis* was the respective lengths of prolateral setae relative to the distances between their bases. In *T. mcgregori* the setae are equal to or slightly longer than the distances between their bases, and distinctly shorter than the bases in *T. flumenis*. In 1974, Chant also used the elongated cervix of the spermathecae and the absence of a plate for the third pair of sternal setae as effective separating characters. Muma (1963) stated that *T. mcgregori* could be separated from *T. flumenis* if the length of $L_8$ was slightly less than twice the distance between $L_8$ and $L_9$, and if $M_2$ failed to extend beyond the base of $L_8$. Utah specimens failed to satisfy Muma's (1963) criteria, but since they agree with the other three authors, they are considered to be *T. mcgregori*.

This species has been reported from Mexico and Canada (Chant 1959), as well as numerous localities in the United States: Alaska, Maryland, Virginia, Ohio, and western United States (Chant et al. 1974), Florida (Muma 1963, Muma and Denmark 1970), California, Arizona, Nevada, New Mexico, and Washington (Schuster and Pritchard 1963), Missouri (Poe and Enns 1969), and Oregon and Utah (Jorgensen 1964, 1967, Leetham and Jorgensen 1969).

Although *T. mcgregori* was reported in North America as early as 1953 (Cunliffe and Baker 1953), it wasn't until Croft and Jorgensen (1969) reported on its life history that any biology was known. This predator has been shown to feed on *Tetranychus pacificus* and *Eotetranychus wallamettei* (Schuster and Pritchard 1963, Schuster 1966), *Panonychus ulmi* (Poe and Enns 1969, Croft and Jorgensen 1969), *Tetranychus urticae* and *Bryobia rubrioculus*, the latter being preferred in Croft and Jorgensen's (1969) work. Croft and Jorgensen (1977) later found *Aculus schlectendali* to be essential to significant predation on *B. rubrioculus*, but reported the former to be its preferred prey. *Typhlodromus mcgregori* also develops larger numbers when feeding on the eriophyids *Aculus coronutus* and *Eriophyes pyri* (Croft and Jorgensen 1977). They inhabit all portions of apple trees as well as cover, litter, and soil beneath them (Leetham and Jorgensen 1969, Dodoo 1968, Poe and Enns 1969). In addition they have been reported from grape (Schuster 1966, Flaherty and Huffaker 1970) and *Malva* sp. (Muma and Denmark 1970). In Utah they have been collected from apple leaves, bark, spurs, and cover and litter beneath the trees in all counties sampled.

Their potential as agents in an integrated pest management program has been questioned by Duke et al. (1970) and Croft and Jorgensen (1969, 1977) because (1) they are tied too closely to *B. rubrioculus* and *A. schlectendali* in abandoned orchards, (2) their distribution is not efficiently correlated with most pests, (3) their population growth is slow, and (4) their searching behavior restricts contact with most prey species.

### *Typhlodromus occidentalis* (Nesbitt)

Figs. 26, 27

Chant et al., 1974:1276, Figs. 34–27

Dorsal plate oval, highly reticulate in female, especially posterior portion. Dorsal setae sometimes slightly plumose, usually longer than distances from their bases to bases of nearest succeeding neighbors. $D_6$ minute, $S_2$ absent, $S_1$ shorter than associated laterals and sometimes slightly plumose. Peritremes short, extending nearly to $L_5$, about two-thirds distance between $L_5$ and $L_6$.

Although descriptions of the Utah specimens fail to completely satisfy those provided by Nesbitt (1951), Chant (1959), and Schuster and Pritchard (1963), they are completely agreeable with descriptions by Kennett (1958), Muma (1963), and Chant et al. (1974). Utah specimens are generally larger than others (Hoying and Croft 1977), but they fall within the variation reported by David (1970). They also satisfy the morphological analyses reported by Hoying and Croft (1977) in their comparative studies of *T. occidentalis* and *Typhlodromus longipilus.*

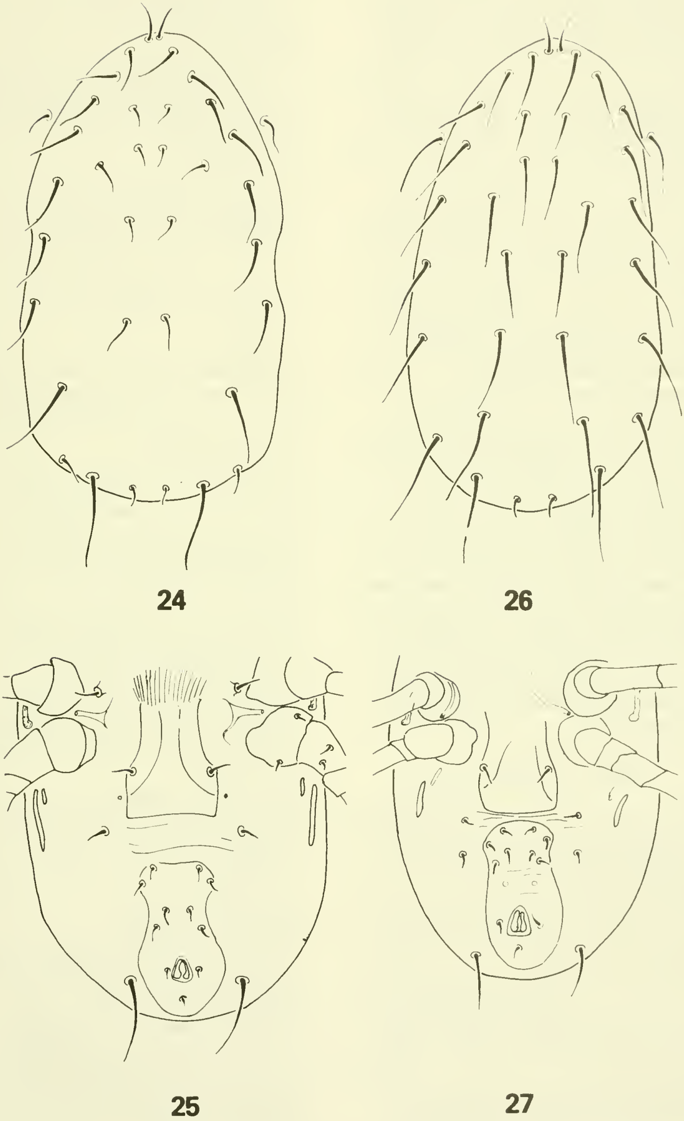
*Typhlodromus occidentalis* has been reported from all regions of temperate North America, although they were most frequently reported from western United States (Chant 1957, 1959, Chant et al. 1974, Anderson et al. 1958, Schuster and Smith 1960, Schuster and Pritchard 1963, and Muma 1963). After careful study Hoying and Croft (1977) reported *T. occidentalis* from only western North America, possibly being replaced by *T. longipilus* in the more humid east. In Utah, they were found wherever derelict orchards were sampled and in most commercial orchards.

This nearly ubiquitous species was first studied by Nesbitt (1951), but shortly thereafter several life history studies were reported (Lee and Davis 1968, Laing 1969, Croft and McMurtry 1972). They have been reported to feed on *Tetranychus telarius* (Nesbitt 1951, Kenneth 1958, Leigh 1963, Muma 1963, Schuster and Pritchard 1963), *Tetranychus willamettei* (Schuster and Pritchard 1963, Flaherty and Huffaker 1970), *Tetranychus pacificus* (Schuster and Pritchard 1963, Chant 1961, Croft and McMurtry 1972, Flaherty and Huffaker 1970), *Tetranychus urticae* (Chant 1961, Croft and McMurtry 1972, Lee and Davis 1968), and *Tetranychus mcdanieli* (Hoyt 1969). Apparently there are distinct strains, possibly resulting from varying insecticide schedules (Croft and McMurtry 1972). Comparative studies of these strains have been reported for reproductive isolation (Croft 1970) and pesticide resistance (Croft and Barnes 1972). Their "host" plants are so varied and numerous that itemizing them would not be particularly useful, because they can be expected to occur on almost any plant where their varied prey species occur. In Utah they have been collected from apple leaves, bark, and spurs, as well as cover beneath apple leaves. Collections have been made in Utah, Salt Lake, Uintah, Cache, San Juan, and Emery counties.

This species has shown some capacity to provide economic control of tetranychid species if managed properly (Lee and Davis 1968, Leetham and Jorgensen 1969, Hoyt 1969a, 1969b, Croft 1975a, 1975b, 1975c), although Anderson and Morgan (1958a) had considered it rather unlikely earlier. At the present time, *T. occidentalis* has more apparent potential than any of the other species in integrated pest management programs in Utah.

## SUMMARY

The control of mite pests in Utah apple orchards has been reviewed in a series of topical papers by Davis (1955, 1956, 1959, 1967, 1970) and Jorgensen (1967). We have attempted to consolidate existing information along with much that is new to establish the basis of our present knowledge. Phytoseiid mites were collected from commercial and derelict apple orchards throughout the past and present major fruit-growing areas of Utah. Mites were collected from as many



Figs. 24–27. Dorsal (24) and ventral (25) views of *Typhlodromus mcgregori*, and dorsal (26) and ventral (27) views of *Typhlodromus occidentalis*.

habitats as possible and during all seasons.

Twelve species were collected and identified; some were rather infrequently recorded, and others were almost ubiquitous throughout the state. Least common were *A. floridanus, A. oregonensis, A. rosellus,* and *T. smithii*; common were *A. salish, A. fallacis, A. ovatus,* and *T. caudiglans*; and most common were *A. cucumeris, T. columbiensis, T. mcgregori,* and *T. occidentalis*. Only *A. fallacis, A. cucumeris, T. caudiglans, T. mcgregori,* and *T. occidentalis* have had sufficient life history research reported to assess their potential value as integrated agents into pest management programs. Additional work is essential for a complete understanding of most species, but may not be advisable as one considers their projected potential.

*Amblyseius fallacis* and *T. occidentalis* each have proven to be valuable in integrated pest management programs. This is partially due to their developed resistance to organic phosphate pesticides, but they also have biological qualities that assist their usefulness. Future research would seem to be best if directed to integrating these two species more completely into possibly pest management programs in Utah rather than working with species with less potential. *Typhlodromus occidentalis* is already partially successful where managed properly, but a great deal more work needs to be done with *A. fallacis* in Utah.

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# SUBSPECIES SPECIFICITY OF GALL FORMS ON *CHRYSOTHAMNUS NAUSEOSUS*

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ABSTRACT.— Galls induced by tephritid flies (Diptera: Tephritidae) on *Chrysothamnus nauseosus* ssp. *albicaulis*, *consimilis*, *graveolens*, and *salicifolius* are useful in taxonomic identification of these subspecies in Utah. In this study, "callus" galls were found almost exclusively on ssp. *albicaulis*. "Cotton" galls were more frequent on ssp. *consimilis* and *graveolens*. "Mace" galls occurred on all four subspecies but were the only gall found on naturally occurring populations of ssp. *salicifolius*. Gall form specificity is not as well correlated with *C. nauseosus* subspecies in peripheral areas of the species range as in Utah. This decrease in specificity may be due to decreased competition for the host plant in outlying areas.

*Chrysothamnus nauseosus*, rubber rabbitbrush, is a shrub that is widely distributed in western North America. The shrub occurs from British Columbia and Saskatchewan south to west Texas and Baja California on plains, valleys, and foothills (Hall and Clements 1923). It is most abundant in the central portion of its range, the intermountain area, including all of Utah, most of Nevada, eastern California, southeastern Oregon, southern Idaho, southwestern Wyoming, and western Colorado (Cronquist et al. 1972, Hanks et al. 1975). *Chrysothamnus nauseosus* is often associated with *Artemisia tridentata*, big sagebrush, and is also a frequent component of salt desert shrub communities (Branson et al. 1976, McArthur et al. 1979).

*Chrysothamnus nauseosus* includes 15 subspecies (Anderson 1966, 1971, Anderson et al. 1974). In Utah, four common subspecies are *albicaulis*, *consimilis*, *graveolens*, and *salicifolius* (Hanks et al. 1975). Each of these subspecies has preferred habitats (Plummer 1977), but occasionally two or more subspecies may be found together in the same area. Some introgression occurs at these sites (Hanks et al. 1975), but hybridization and introgression are minimized because self-pollination is prevalent in *Chrysothamnus* (Anderson 1966, McArthur et al. 1978). The various subspecies of *C. nauseosus* have different forage values in natural stands and different uses in revegetation efforts (McArthur et al. 1974, Hanks et al. 1975, Plummer 1977). There is considerable intraspecific variation in plant morphology (Hall and Clements 1923, Cronquist 1975), which makes subspecific taxonomic identification of individual plants sometimes difficult.

During the winter of 1975–76, we noted that in some Utah areas tephritid-induced galls of different forms had absolute *C. nauseosus* subspecies specificity. This study was undertaken to see how widespread and how absolute the gall form specificity was on *C. nauseosus* ssp. *albicaulis*, *consimilis*, *graveolens*, and *salicifolius*. It was thought that if these gall forms were subspecies-specific, they could help in subspecies identification, and in the management of the various subspecies. In the course of our data collection we learned that J. K. Wangberg was studying the biology of tephritid gall formers on *Chrysothamnus* (Wangberg 1976), and we compared our results with his.

## MATERIALS AND METHODS

Gall form specificity was measured (1) at five sites where two subspecies naturally grow together (Table 1); (2) at the Snow Field Station, Ephraim, Utah, where *Chrysothamnus nauseosus* ssp. *albicaulis*, *consimilis*, *graveolens*, and *salicifolius* are growing in a uniform garden; and (3) in more or less pure natural stands of the four subspecies (Table 2). In addition, gall types were observed at more than 30 other sites in Utah and northern Arizona.

We looked at three gall forms (Fig. 1):

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Table 1. Gall frequencies from mixed populations at five Utah localities.

| Collection information | | |
|---|---|---|
| Subspecies[1] | Authors' number | Site |
| Chna$^{a}$ | 759 | Big Rock Candy Mountain, Sevier Co.[3,4] |
| Chna$^{c}$ | 760 | Big Rock Candy Mountain, Sevier Co.[4] |
| Chna$^{a}$ | 770 | 3 km S Fountain Green, Sanpete Co.[4] |
| Chna$^{c}$ | 979 | 3 km S Fountain Green, Sanpete Co.[4] |
| Chna$^{a}$ | 791 | 3 km W Goshen, Utah Co.[4] |
| Chna$^{c}$ | 790 | 3 km W Goshen, Utah Co.[4] |
| Chna$^{a}$ | 811 | 1 km W Paragonah, Iron Co. |
| Chna$^{g}$ | 812[5] | 1 km W Paragonah, Iron Co. |
| Chna$^{a}$ | 818 | Gould Wash, Washington Co.[4] |
| Chna$^{g}$ | 817 | Gould Wash, Washington Co.[4] |

[1] Subspecies symbols: Chna$^{a}$ = *Chrysothamnus nauseosus* ssp. *albicaulis*; Chna$^{c}$ = *C. n.* ssp. *consimilis*; Chna$^{g}$ = *C. n.* ssp. *graveolens*.

[2] $\bar{x} \pm$ sd = mean ($\bar{x}$) ± standard deviation (sd) of number of galls on terminal 15 cm of a random branch/plant.

[3] Some plants of intermediate morphology were found.

[4] Browsing preference for ssp. *albicaulis* noted. Browsers were deer at Big Rock Candy Mountain, sheep at Fountain Green, horses and cattle at Goshen, and cattle and deer at Gould Wash.

[5] Gall frequencies significantly different with $p<0.01$.

1. The "callus" gall, which is more or less glabrous, round to ovoid, 0.3 to 1.2 cm in diameter, and persistent up to two years on the plant.

2. The "cotton" gall, which is covered with a thick, white tomentum, round to ovoid, 0.7 to 1.4 cm in diameter, and generally not as persistent as the callus gall, although some galls persist for two years.

3. The "mace" gall, which is usually glabrous, round to ovoid, 0.5 to 1.2 cm in diameter, and covered with small bracts. Persistence of the mace gall past the first year is unknown.

Active galls are those containing larvae; whereas inactive galls are those from which the flies have emerged.

Gall frequencies were scored at collection sites by counting the galls (active and inactive) on the terminal 15 cm of a randomly selected branch of each mature shrub (>30 cm tall) on more or less straight line transects through *C. nauseosus* populations. Fifty plants were scored in each of the pure stands. At the mixed sites 50 plants of each subspecies were scored as the plants occurred on the transects. All data collection and observations were made in the winter and early spring of 1976–77.

*Chrysothamnus nauseosus* subspecies were identified using Anderson's (1973) key at the time of data collection or during the following summer when leaves were present on the plants. Herbarium vouchers have been deposited at the Shrub Sciences Laboratory Herbarium (SSLP) in Provo, Utah. Flies were reared to maturity from a few galls, and were identified using Wangberg's (1976) key.

A paired *t* test (Woolf 1968) was used to test the significance of gall form frequency differences where two gall types occurred on the same subspecies (Table 1).

## Results and Discussion

Correlation of gall morphology with *Chrysothamnus nauseosus* subspecies.— The five study areas of Table 1 reflect almost complete gall form specificity for each subspecies. In each case *C. nauseosus* ssp. *albicaulis* is growing with either *C. nauseosus* ssp. *consimilis* or ssp. *graveolens*. The cotton gall was found only on ssp. *consimilis* and ssp. *graveolens*. The callus gall, except for a single plant at the Paragonah site, was found only on ssp. *albicaulis*. Both ssp. *consimilis* and ssp. *graveolens* tend to have greener stems and less leaf and stem tomentum than ssp. *al-*

| Gall type | | | | | |
|---|---|---|---|---|---|
| Callus | | | Cotton | | |
| $\bar{x} \pm sd^2$ | Range of values | Percent of plants w/galls | $\bar{x} \pm sd^2$ | Range of values | Percent of plants w/galls |
| 7.92 ± 8.55 | 0–34 | 80 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 |
| 1.00 ± 1.76 | 0–9 | 46 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0.70 ± 0.90 | 0–3 | 50 |
| 4.32 ± 4.83 | 0–18 | 80 | 0 | 0 | 0 |
| 0 | 0 | 0 | 4.44 ± 6.18 | 0–23 | 58 |
| 6.02 ± 4.83 | 0–21 | 94 | 0 | 0 | 0 |
| 0.04 ± 0.28 | 0–2 | 2 | 5.36 ± 2.98 | 0–11 | 98 |
| 5.56 ± 5.00 | 0–21 | 90 | 0 | 0 | 0 |
| 0 | 0 | 0 | 3.50 ± 6.45 | 0–14 | 80 |

*bicaulis.* The exceptional Paragonah plant could well have been an introgressant. At the Big Rock Candy Mountain site galls were not found on the ssp. *consimilis* plants (Table 1). However, a few plants of intermediate morphology were located—they had callus galls.

At the Snow Field Station the four subspecies of *C. nauseosus* are growing in a uniform garden. There callus galls were found on ssp. *albicaulis*, and cotton galls were found, although much less frequently, on the other three subspecies.

In the uniform population studies (Table 2), only callus galls were observed for *C. nauseosus* ssp. *albicaulis*, and only cotton galls were observed for ssp. *consimilis*. Cotton galls were most common on ssp. *graveolens*, although a few mace galls were found on this subspecies at the Hanksville site. Only mace galls were observed on ssp. *salicifolius*.

At sites where observations were made but gall frequency data were not recorded, we rarely found exceptions to the data presented in Table 2. A population of ssp. *albicaulis* (collection number: McArthur, Tiernan, and Welch 769) located 3 km south of Nephi, Juab Co., Utah, had a single plant corresponding to ssp. *consimilis*. Whereas the ssp. *albicaulis* plants had high numbers of callus galls, the aberrant ssp. *consimilis* plant had only a single gall, which was a callus gall.

Galls were much more common in some areas than in others. For example, ssp. *albicaulis* plants near Ogden Bay, Weber Co., Utah (McArthur 786), were nearly devoid of galls; whereas a few miles south, on the north end of Antelope Island, Davis Co., Utah, plants of the same subspecies (McArthur 789, Table 2) were heavily infested with galls. In the upper Sevier Valley, ssp. *consimilis* plants lacked galls, but in the lower Sevier Valley and in Sanpete Valley (a Sevier Valley tributary) they had cotton galls. A few mace galls were found with more numerous callus galls on ssp. *albicaulis* in Willow Creek Canyon, north of Richfield, Sevier Co., Utah.

Mace galls were found on all four subspecies in at least one location of our observations. The mace galls were encountered less frequently and had a lower incidence per plant than the other two types of galls.

East of Ephraim, Sanpete County, Utah, we found both ssp. *albicaulis* (McArthur 779) and ssp. *consimilis* (McArthur 780) growing with several plants of intermediate morphology (McArthur 781). There, callus galls were on ssp. *albicaulis* plants; cotton galls were on ssp. *consimilis* plants; and both kinds of galls were found on a few plants of intermediate morphology.

Wangberg (1976) found that the tephritid fly (*Aciurina bigeloviae*) was responsible for galls whose descriptions match those of the callus and mace forms discussed in this report. Another tephritid (*A. maculata*) was responsible for galls matching the description

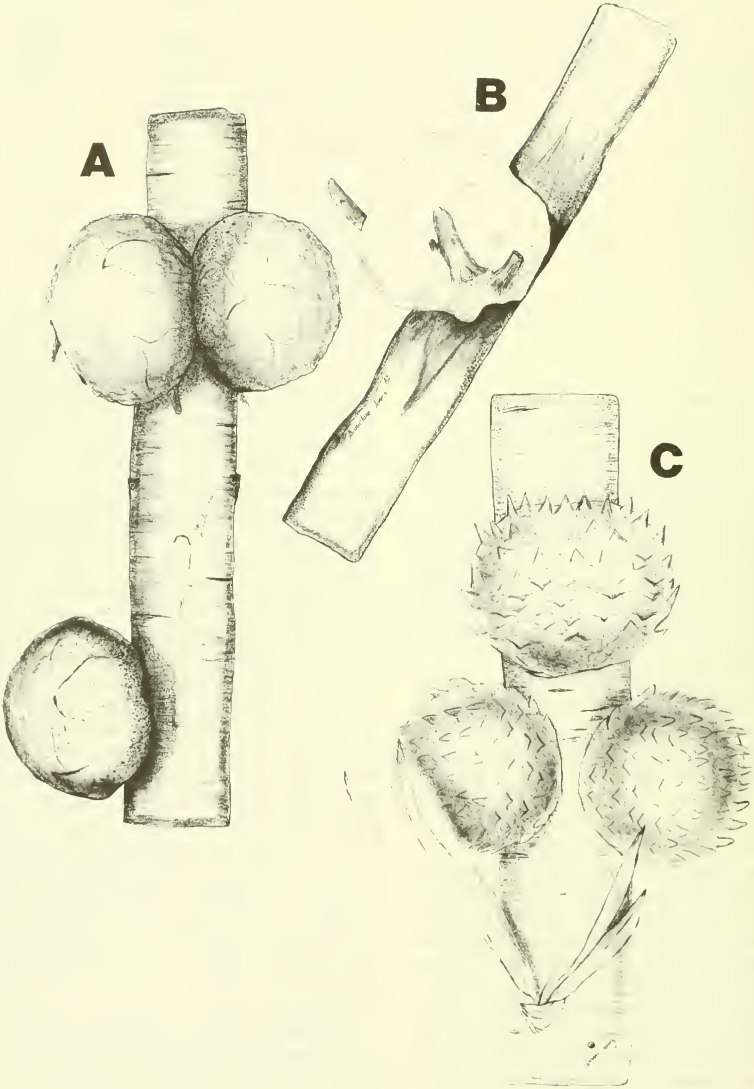

Fig. 1. Drawings of gall forms. A. callus. B. cotton. C. mace. (4X).

of the cotton gall. Wangberg (1976) described the galls but did not use the terms cotton, callus, or mace. He (Wangberg 1976) stated that in Idaho both cotton and callus gall forms were found on *C. nauseosus* ssp. *albicaulis* and ssp. *consimilis*. Observations made during this study in Utah (Tables 1 and 2) and northern Arizona were quite different. The callus gall was very specific for ssp. *albicaulis*. The cotton gall was specific for ssp. *consimilis* and *graveolens* at most locations. Cotton galls were found on ssp. *albicaulis* only where the callus gall was absent. For example, in northeastern Mohave Co., Arizona, and western Kane Co., Utah, ssp. *albicaulis*, *graveolens*, and *consimilis* all had cotton galls (McArthur 819, 820, 832). Mace galls were much rarer than callus or cotton galls in most areas of observation (Tables 1 and 2), but were occasionally found on all four subspecies of *C. nauseosus*.

The relationship between gall tomentum and plant tomentum is perplexing. Glabrous callus and mace galls have specificity for ssp. *albicaulis* and ssp. *salicifolius*, respectively. These subspecies have looser and more obvious tomentum than ssp. *consimilis* and *graveolens*, which show specificity for the tomentulose cotton gall.

Taxonomic indicator value of gall forms on *C. nauseosus* subspecies.— The callus gall form is specific for *C. nauseosus* ssp. *albicaulis* in most of Utah. If a callus gall is present on *C. nauseosus*, the plant is in all likelihood ssp. *albicaulis* (Table 1 and 2). In winter, when leaves are lacking from *C. nauseosus*, callus galls help distinguish ssp. *albicaulis* from ssp. *consimilis* and ssp. *salicifolius*. In Idaho apparently, this specificity does not occur (Wangberg 1976).

The cotton gall, in Utah, is found most commonly on ssp. *consimilis* and *graveolens* (Tables 1 and 2). However, in the few areas where the callus gall is missing the cotton gall may be found on ssp. *albicaulis*. The cotton gall has not been found on naturally

Table 2. Gall frequencies in uniform populations at nine Utah localities.

| Collection information | | | Gall type | Frequency | | |
|---|---|---|---|---|---|---|
| Subspecies[1] | Authors' number | Site | | $\bar{x} \pm$ sd[2] | Range of values | Percent of plants w/galls |
| Chna$^{a}$ | 768 | Mouth of Chicken Creek Canyon, Juab Co. | Callus | 2.03 ± 3.34 | 0–18 | 72 |
| Chna$^{a}$ | 773 | 3 km S. Bluffdale, Salt Lake Co. | Callus | 1.80 ± 2.03 | 0–8 | 60 |
| Chna$^{a}$ | 789 | N. end Antelope Island, Davis Co. | Callus | 5.10 ± 7.26 | 0–43 | 74 |
| Chna$^{c}$ | 962 | Pigeon Hollow, Sanpete Co. | Cotton | 1.24 ± 1.41 | 0–6 | 68 |
| Chna$^{c}$ | 976 | 3 km NE. Ephraim, Sanpete Co. | Cotton | 1.06 ± 1.05 | 0–4 | 68 |
| Chna$^{g}$ | 1000 | Hanksville, Wayne Co.[3] | Cotton[3] | 1.44 ± 1.69 | 0–7 | 66 |
| Chna$^{s}$ | 964 | Snowberry Exclosure, Ephraim Canyon, Sanpete Co. | Mace | 0.18 ± 0.52 | 0–3 | 14 |
| Chna$^{s}$ | 1061 | Red Creek, Duchesne Co. | Mace[4] | 0.26 ± 0.49 | 0–2 | 24 |
| Chna$^{s}$ | 1066 | Moon Lake, Duchesne Co. | Mace | 0.16 ± 0.55 | 0–3 | 10 |

[1] Subspecies symbols: Chna$^{a}$ = *Chrysothamnus nauseosus* ssp. *albicaulis*; Chna$^{a}$ = *C. n.* ssp. *consimilis*; Chna$^{g}$ = *C. n.* ssp. *graveolens*; Chna$^{s}$ = *C. n.* ssp. *salicifolius*.

[2] $\bar{x} \pm$ = mean ($\bar{x}$) ± standard deviation (sd) of number of galls on terminal 15 cm of a random branch/plant.

[3] Two morphologies of ssp. *graveolens* present. A low incidence of mace galls was observed but not recorded.

[4] One poorly defined cotton gall was observed.

growing populations of ssp. *salicifolius*, but was found on plants of this subspecies transplanted to the Snow Field Station. Subspecies *salicifolius* is ordinarily a mountain taxon, whereas the Snow Field Station is in a valley setting.

The mace gall has been found on all four subspecies but is the only one of the three galls found on naturally occurring populations of ssp. *salicifolius* (Table 2).

Resource partitioning by the gall-forming tephritid flies.— Wangberg (1976) discussed the problem of niche-sharing by fly species that induce galls on similar parts of the same subspecies of *C. nauseosus* at the same time of the year. Wangberg believed, following Darlington (1972), that tephritid fly species compete in nature and divide the resource. Our studies support such a competitive division of the plant resource. Our study showed more gall-form specificity on *C. nauseosus* subspecies than Wangberg's (1976), perhaps because our study was in the central area of *C. nauseosus*'s range, where there are larger concentrations of the plant than are present where Wangberg studied (Hall and Clements 1923). L. C. Anderson (letter dated 16 February 1978) has data indicating less specificity for gall forms on plants growing outside of Utah than on those growing in Utah. In the central area of the host species' occurrence, the gall formers might be better off to be host specific to avoid competition with large populations of various taxa of gall-forming flies. In outlying areas such host specificity might be a disadvantage because host plants would be rarer. Moreover, gall-forming fly populations would not be as high, so competition would be reduced. MacArthur (1972:17) touched on this problem when he stated that species are more likely to compete in localities where an advantage can be gained.

Another possible explanation for gall-form specificity is that different gall forms are not a response to different fly species but rather a response to the host plant species. We have not reared enough fly specimens to address this possibility. However, we think this explanation is unlikely, because a few individual plants had more than one gall form.

## Acknowledgments

This study was facilitated by federal funds for wildlife habitat restoration made available from the Pittman-Robertson W-82-R Project (Cooperators: Intermountain Forest and Range Experiment Station, USDA Forest Service, Ogden, Utah; and Utah State Division of Wildlife Resources, Salt Lake City, Utah). The Snow Field Station is cooperatively maintained by the above agencies, Utah State University, and Snow College. The drawings of Figure 1 were made by Annielane Jones Yazzie. Drs. L. C. Anderson, D. L. Hanks, K. T. Harper, and J. K. Wangberg provided technical advice.

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# HOMING BY A PYGMY RABBIT[1]

Jeffrey S. Green[2,3] and Jerran T. Flinders[2]

Abstract.—A juvenile female pygmy rabbit (*Sylvilagus idahoensis*) escaped from a holding pen and was recaptured 211 days later 200 m from its original capture site and 2.5 km from the pen facility.

Homing for distances of 3.8 km (Hill 1967) and 4.8 km (Bowers 1954) was reported for the eastern cottontail (*Sylvilagus floridanus*). Chapman (1971) reported the brush rabbit (*S. bachmani*) failed to home greater than 0.16 km in 29 trials. This is a report of homing by a pygmy rabbit (*S. idahoensis*), the smallest member of the genus, from a distance of 2.5 km.

The rabbit, a juvenile female weighing 101 g, was captured 23 June 1977 on the U.S. Sheep Experiment Station near Dubois, Idaho. It was taken to a permanent pen facility, ear-tagged, and placed in a cage from which it escaped during the first night. Two hundred and eleven days later on 20 January 1978, while trapping pygmy rabbits for behavioral research, the escaped specimen was caught approximately 200 m from its original capture site and 2.5 km from the pen facility. It appeared to be in good condition and it weighed 392 g. The rabbit was observed at least four times during the next 19 days in the second capture area and was apparently a resident there. Suitable habitats occupied by pygmy rabbits are found in any direction of escape from the cage area. The fact that the animal traveled toward its original capture site is, therefore, not apparently related to the absence of suitable habitat elsewhere.

Maximum movements we previously recorded for two pygmy rabbits (tracked in snow) were one-way distances of 140 and 450 m during winter 1976. Wilde et al. (1976) noted an adult female (radio-instrumented in late November) that showed extreme fidelity to her burrow and was never located farther than 20 m from the burrow where originally captured. However, they documented longer movements by tagged and recaptured individuals; one female moved a maximum of 300 m, a male moved as far as 500 m, and another male moved 200 m. Janson (1946) observed that activity of pygmy rabbits in winter was within a radius of about 27 m from their burrows. He wrote that in spring the radius of activity increased in response to snow melt and onset of breeding activity. On the basis of McNab's (1963) method of predicting approximate size of home range from basal metabolism and body size of mammals, the home range of the pygmy rabbit should be about 0.8 ha. This was calculated using an average body weight of 454 g obtained from 11 female pygmy rabbits kept in captivity and weighed at least weekly from September through February. Clearly the movement we recorded is far beyond that normally associated within a radius of movement well within documented range for the species. A movement of 2.5 km for a juvenile sheds light on the dispersal and pioneering capabilities of the pygmy rabbit.

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[1] This study was supported by USDA Western Region Federal Cooperative Agreement 12-14-5001-264.

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# BEETLES FROM THE ENVIRONS OF LAKE POWELL IN SOUTHERN UTAH AND NORTHERN ARIZONA

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Abstract.— Sixty-eight species of beetles of 14 families were collected in pit traps in 12 major vegetative communities during environmental monitoring studies in the summers of 1971 to 1973 in southern Utah and northern Arizona. Seasonal and plant community differences and correlations in population and composition were noted for the 16 sites studied. Highest populations and the most species were found in a grass community, but occurred in different months in each of the three years. Lowest populations were found in a *Coleogyne* community, and fewest species in an *Artemisia*-grass community.

In June 1971 an ecological study was initiated by the Center for Health and Environmental Studies at Brigham Young University to establish baselines to determine the environmental effects of the Navajo Generating Station near Page in northern Arizona, and the proposed Kaiparowits Generating Station in southern Utah.[2] Field studies of arthropods were conducted from July to September in 1971, and from May to August in 1972 and 1973.

Can pit traps (an outer galvanized metal sleeve 18 cm in diameter and 36 cm long with a stainless steel, flanged inner can of slightly smaller size) were used to capture ground-dwelling arthropods. Five traps 30 m apart were placed on each of two transects, which were 45 m apart. These were left open, dry, and unbaited for a 72-hour period once each summer month. Of the 12 sites studied in 1971, the 16 in 1972, and the 12 in 1973, some were studied only one year, others two, and some all three years. Beetles, other arthropods, small rodents, and lizards were collected from the cans daily while they were open for trapping studies. The beetles were identified by Dr. Vasco M. Tanner.

## Study Sites and Their Predominant Vegetation

Site 1. *Ephedra-Vanclevea-Sporobolus-Oryzopsis-Hilaria.* Base N slope Cedar Mtn, 5 km W Glen Cnyn City, Kane Co., Utah.

Site 2. *Juniperus-Ephedra-Muhlenbergia-Bouteloua-Hilaria-Oryzopsis.* Cedar Mtn, 6.5 km S site 1.

Site 3. *Ephedra-Hilaria-Bouteloua-Oryzopsis.* Cedar Mtn, 2 km S site 2.

Site 4. *Coleogyne-Ephedra-Atriplex-Chrysothamnus.* Cedar Mtn, 1.3 km SE site 3.

Site 6. *Artemisia-Hilaria-Aristida-Oryzopsis.* Smokey Mtn, 23 km from Last Chance Jnct, Kane Co., Utah.

Site 8. *Grayia-Ephedra-Coleogyne-Hilaria-Bouteloua-Oryzopsis.* Smokey Mtn, 14.5 km from Last Chance Jnct., Kane Co., Utah.

Site 10. *Ephedra-Yucca-Eurotia-Vanclevea-Oryzopsis-Streptanthella.* Ahlstrom Pnt Rd., 7.5 km S junct., Kane Co., Utah.

Site 13. *Grayia-Ephedra-Oryzopsis-Bouteloua-Hilaria.* Nipple Bench, 6.5 km SE Tibbet Spring, Kane Co., Utah.

Site 14. *Coleogyne-Grayia-Ephedra-Chrysothamnus-Hilaria.* 3 km S site 13.

Site 19. *Coleogyne.* 15 km S Page, Coconino Co., Arizona by Hwy 89.

Site 20. *Muhlenbergia-Bouteloua-Hilaria.* 19 km S Page, Coconino Co., Arizona by Hwy 89.

Site 22. *Coleogyne-Ephedra-Hilaria.* E Navajo Generating Station, SE Page, Coconino Co., Arizona.

Site 23. *Ephedra-Coleogyne-Grayia-Hilaria.* Cathys Flat, 2 km N Tibbet Spring, thence 2.5 km E, Kane Co., Utah.

Site 27. *Juniperus-Pinus.* Four-mile Bench, 5 km SE cow camp, head Wesses Cnyn, Kane Co., Utah.

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[2] These studies were funded cooperatively by Arizona Public Service, Los Angeles Power and Light, Salt River Project, San Diego Power and Light, and Southern California Edison.

Site 28. *Artemisia-Bouteloua-Plantago*. 3 km E site 27.

Site 30. *Ephedra-Bouteloua-Hilaria-Sporobolus-Salsola*. Brigham Plains Flat, Kane Co., Utah.

## ANNOTATED LIST OF FAMILIES AND SPECIES

### BUPRESTIDAE

*Acamaeodera lanata* Horn: one specimen, 17 July 1972, site 14 (*Coleogyne-Grayia-Ephedra*-grass); 6 specimens, 2 June 1973, site 20 (grass).

### CARABIDAE

*Bembidion* sp.: one specimen, 13 May 1973, site 27 (juniper-pinyon).

*Calosoma triste* Lec.: one specimen, 3 May 1973, site 8 (*Grayia*-grass).

*Calosoma* sp.: one specimen, 5 July 1973, site 10 (*Ephedra*-grass).

*Celia* sp.: one specimen, 5 June 1972, site 3 (*Ephedra*-grass); one specimen 6 June 1972, site 1 (*Ephedra-Vanclevea*-grass).

*Harpalus corpulentus* (Csy.): 6 specimens were taken 4 June 1973 at site 3 (*Ephedra*-grass); 2 specimens 6 June 1973, at site 8 (*Grayia*-grass); and one specimen 9 July 1973 at site 14 (*Coleogyne-Grayia-Ephedra*-grass). The apparent absence of this species in 1972 is unusual, inasmuch as sites 3, 8, and 14 were studied from May through August. Its absence in 1971 is also unexpected, even though collections were made only in July and August.

*Harpalus furtivus* (Lec.): 3 specimens, 21 August 1972, site 28 (*Artemisia*-grass); one specimen, 5 September 1972, site 3 (*Ephedra*-grass).

*Harpalus lustrans* Csy.: 2 specimens, 4 June 1973, site 3 (*Ephedra*-grass); one specimen, 14 June 1973, site 28 (*Artemisia*-grass).

*Harpalus* sp.: one specimen, 10 July 1973, site 23 (*Ephedra-Coleogyne-Grayia*).

*Rhadine jejuna* Lec.: one specimen, 12 June 1972, site 19 (*Coleogyne*).

*Rhadine* sp.: one specimen, 4 July 1973, site 8 (*Grayia*-grass).

*Selenophorus aeneopiceus* Csy.: 3 specimens, 12-13 June 1972, site 19 (*Coleogyne*); one specimen, 22 June 1972, site 30 (*Ephedra*-grass).

### CERAMBYCIDAE

*Moneilema obtusa* Lec.: one specimen, 1 August 1973, site 10 (*Ephedra*-grass).

*Prionus* sp.: one specimen, 7 July 1973, site 30 (*Ephedra*-grass).

### CHRYSOMELIDAE

*Disonycha fumata* (Lec.): 4 specimens, 12-13 July 1971, site 3 (*Ephedra*-grass).

*Disonycha latifrons* Schaffr.: one specimen, 3 May 1973, site 6 (*Artemisia*); one specimen, 6 May 1973, site 30 (*Ephedra*-grass).

### CLERIDAE

*Cymatodera fuchsi* Schaffr.: one specimen, 12 August 1971, site 13 (*Grayia-Ephedra*-grass); one specimen, 10 July 1972, site 10 (*Ephedra*-grass).

### COCCINELLIDAE

*Hippodamia convergens* Guer.: one specimen, 2 June 1973, site 20 (grass).

### COLYDIIDAE

*Bitoma* sp.: one specimen, 26 September 1971, Glen Cnyn City.

### CURCULIONIDAE

*Cimbocera buchanani* Ting: 3 specimens, 13-14 July 1971; one specimen, 10 November 1971, site 3 (*Ephedra*-grass); one specimen, 15 October 1971; one specimen, 9 May 1973, site 14 (*Coleogyne-Grayia-Ephedra*-grass); 3 specimens 14-15 July 1972; one specimen, 14 August 1972, site 20 (grass); one specimen, 10 May 1973, site 23 (*Ephedra-Coleogyne-Grayia*).

*Cimbocera conspersa* Fall: 4 specimens were taken at site 2, one at site 3, one at site 6, 4 at site 14, 2 at site 23, and 12 at site 27. Plants of the genus *Ephedra* were common to four of the six sites where this beetle was found. However, greatest numbers were found in the juniper-pinyon community. Five specimens were taken in April and May 1972, and 19 from May to August 1973. Greatest numbers were found in May of both years. The activity of this species apparently is spring and early summer, for no specimens were taken in July or August of 1971, none after May in 1972, and only four after May in 1973.

*Cimbocera petersoni* Tanner: one specimen, 29 April 1973, site 2 (juniper-*Ephedra*-grass); one specimen, 30 April 1973, site 1 (*Ephedra*-*Vanclevea*-grass).

*Dinocleus angularis* (Lec.): one specimen, 4 May 1973, site 10 (*Ephedra*-grass).

*Eucyllus unicolor* Van Dyke: one specimen, 5 August 1972, site 3 (*Ephedra*-grass).

*Eupagoderes varius* (Lec.): one specimen, 12 July 1972, site 6 (*Artemisia*).

*Eupagoderes* sp.: one specimen, 3 June 1973, site 2 (juniper-*Ephedra*-grass).

*Ophryastes sordidus* Lec.: one specimen, 9 September 1971, site 7 (*Grayia*-*Coleogyne*-grass).

*Ophryastes sulcirostris* (Say): one specimen, 4 June 1973, site 2 (juniper-*Ephedra*-grass).

*Ophryastes* sp.: one specimen, 13 May 1973, site 28 (*Artemisia*-grass).

### HISTERIDAE

*Saprinus discordalis* (Lec.): one specimen, 20 July 1971, Navajo Mtn.

*Saprinus lugens* Et.: 6 specimens were taken at site 2, 4 at site 10, one at site 14, and 23 at site 22. Plants of the genus *Ephedra* were common to three of the four sites where this species was found. However, greatest numbers were found in the *Coleogyne* community. Twenty-three specimens were taken in July 1972, and 5 and 6 in May and July of 1973, respectively. Apparently July is the month of greatest activity of this species, even though none were taken in July of 1971. However, site 2 was the only one of the four sites where this species was found that was studied during July of 1971.

*Saprinus oregonensis* Lec.: 2 specimens, 2 August 1971, site 6 (*Artemisia*).

### MELOIDAE

*Pyrota mylabrina* Cher.: 34 specimens, 24 August 1972, Cottonwood Cnyn, 9 mi N Hwy 89, ex *Chrysothamnus*.

### MELYRIDAE

*Collops femoratus* (Schaffr.): one specimen, 14 July 1971, site 15 (*Populus*-*Tamarix*-*Lycium*).

*Trichochrons zionicus* Tanner: 28 specimens, summer 1972, specific locality unknown.

### PTINIDAE

*Ptinus* sp.: 8 specimens were taken at site 1, one at site 2, 5 at site 14, 2 at site 17, 6 at site 22, and 8 at site 23. Plants of the genus *Ephedra* and grasses were common to four of the six sites. Significant differences between community types were not evident, although greatest numbers were found in those where *Coleogyne* was a predominant. Four specimens were taken in July and August 1971, 18 from April to August 1972, and eight in May and July of 1973. Greatest numbers were found in May of 1972 and 1973.

### SALPINGIDAE

*Conotus lanchesteri* Van Dyke: This was one of the more common beetles. Twenty-one were taken at site 1, 38 at site 2, one at site 7, 6 at site 9, one at site 13, 2 at site 19, 6 at site 22, 3 at site 23, and 2 at site 27. The plant *Ephedra* was common to four of the nine sites, and greatest numbers were found on sites 1 and 2, where it was present. Specimens were taken in July and August 1971, April to September in 1972, and May to August 1973. In 1971 about equal numbers were taken in July and August, in 1972 greatest numbers were found in August, and in 1973 greatest numbers in July and August. No significant differences were noted between the three years, although slightly more numbers were taken in July and August of 1972 than during those months in other years, and more were taken from May to August in 1972 than for comparative months of 1973.

### SCARABAEIDAE

*Aphodius rubidus* (Lec.): 4 specimens were taken at site 2, 13 at site 3, 3 at site 6, 6 at site 8, 6 at site 10, 4 at site 13, 31 at site 14, 2 at site 20, 3 at site 22, and 17 at site 30. The plant *Ephedra* was common to 6 and grasses to 8 of the 10 sites where this beetle was found. Greatest numbers were found on sites 14 and 30, where *Ephedra* and grasses were common. Specimens were taken in April and from June to September in 1972, and from May to July in 1973. Greatest numbers were found in April of 1972 and May of 1973. From May to August, populations were 24 times higher in 1973 than in 1972.

*Diplotaxis subangulata* (Schaffr.): 2 specimens, 16 June 1972, site 13 (*Grayia*-*Ephedra*-

grass); one specimen, 21 July 1972, site 27 (juniper-pinyon).

*Diplotaxis* sp.: one specimen, 6 April 1971; one specimen, 6 June 1971, site 3 (*Ephedra*-grass); one specimen, 5 June 1971, site 1 (*Ephedra-Vanclevea*-grass).

*Polyphylla diffracta* (Csy.): 3 specimens, 20 July 1971, Navajo Mtn.

*Polyphylla 10-lineata* (Say): one specimen, 12 June 1973, site 23 (*Ephedra-Coleogyne-Grayia*).

*Serica* sp.: one specimen, 11 June 1973, site 13 (*Grayia-Ephedra*-grass); 4 specimens, 19 June 1972; 5 specimens, 20 June 1972, site 27 (juniper-pinyon).

### TENEBRIONIDAE

*Araeoschizus dicipiens* (Horn): one specimen, 7 April 1972, site 1 (*Ephedra-Vanclevea*-grass); one specimen, 13 June 1972, site 19 (*Coleogyne*); one specimen, 9 August 1973, site 30 (*Ephedra*-grass).

*Chilometopon abnorme* Horn: 13 specimens were taken at site 1, one at site 2, 9 at site 4, one at site 6, 2 at site 7, one at site 8, 56 at site 10, 2 at site 13, 4 at site 14, 8 at site 17, and 2 at site 18. These beetles were taken from a variety of vegetative types, but significantly greater numbers were found at site 10, an *Ephedra*-grass community. Specimens were taken from July to September in 1971, May to August in 1972, but only in August of 1973. Beetles in July and August of 1971 were twice as abundant as in 1972, and 48 times as abundant as in 1973. From May to August, they were 30 times as abundant in 1972 as in 1973.

*Coniontis opacus* Horn: one specimen, 13 July 1971, site 4 (*Coleogyne*).

*Coniontis sp.*: one specimen, 6 May 1972, site 4 (*Coleogyne*).

*Edrotes leechi* Doyen: one specimen, 4 June 1972, site 2 (juniper-*Ephedra*-grass); one specimen, 14 July 1971, site 3 (*Ephedra*-grass); one specimen, 12 July 1971, site 4 (*Coleogyne*); one specimen, 11 July 1972, site 6 (*Artemisia*); one specimen, 19 July 1971, site 18 (*Coleogyne*); 2 specimens, 14 August 1972, site 20 (grass); 2 specimens, 12 April 1973; one specimen, 12 May 1972, site 22 (*Coleogyne*).

*Eleodes caudifera* Lec.: 7 specimens were taken at site 1, 2 at site 3, 6 at site 10, 7 at site 13, 3 at site 14, and one at site 19. *Ephedra* and grasses were predominant plants at 5 of the 6 sites. No site had significantly greater numbers of beetles than another. Specimens were taken in July and August 1971, May to July 1972, and May and June 1973. In 1973, greatest numbers were found in May, but no significant differences were noted between months of other years except from May to August, when eight times as many beetles were found in 1973 as in 1972.

*Eleodes extricata* (Say); Beetles of this species were some of the most common and widespread of those taken. A total of 164 specimens was taken from 15 of the 19 sites studied. Greatest numbers were found at sites 3, 19, 20, and 22, which are predominantly *Coleogyne* or grass habitats. Specimens were taken in July and August of 1971, April to September in 1972, and May to August in 1973. Greatest numbers were taken in August and September of 1972, and July of 1973. In July and August of 1972 and 1973 these beetles were about equally abundant, but only one-tenth as abundant in 1971. For the period of May to July, they were about equally as abundant in 1972 as in 1973.

*Eleodes hispilabris sculptilis* Blais.: Beetles of this species were common and widespread; 105 were taken from 13 study sites. Greatest numbers were found at site 10, an *Ephedra*-grass community. In 1971 they were found from July to September, most abundantly during the latter month; in 1972 during April and from June to September, also most abundantly during September; and in 1973 from May to August, mostly in July. In July and August, they were half again as abundant in 1971 as in 1972 and 1973. They occurred in about equal numbers for the period of May to August in 1972 and 1973.

*Eleodes immunis interstitralis* Blais.: one specimen, 18 July 1971, site 17 (grass); one specimen, 19 July 1971, site 1 (*Ephedra-Vanclevea*-grass).

*Eleodes leechi* Tanner: one specimen, 20 July 1972; one specimen, 22 July 1972, site 28 (*Artemisia*-grass); one specimen, 11 July 1973, site 27 (juniper-pinyon); one specimen, 3 August 1973, site 14 (*Coleogyne-Grayia-Ephedra*-grass); 2 specimens, 4 August 1973, site 2 (juniper-*Ephedra*-grass).

*Eleodes obscura sulcipennis* Mann.: These beetles were relatively abundant and widespread and were found on 15 sites. They were most abundant at sites 2, 3, 8, 14, and 19, principally where grasses were predominant. Beetles were taken from July to September, mostly August in 1971; from April to September in about equal numbers each month in 1972; and from June to August, also in about equal numbers each month in 1973. In July and August, populations were three times as high in 1971 as in 1972 and 1973. From May to August about equal numbers were taken in 1972 and 1973.

*Eleodes omissa pygmaea* Blais.: 14 specimens, July and August 1971, site 3 (*Ephedra*-grass); one specimen, 1 August 1971, site 6 (*Artemisia*); one specimen, 11 August 1971, site 13 (*Grayia-Ephedra*-grass); 2 specimens, 11, 13 August 1971, site 14 (*Coleogyne-Grayia-Ephedra*-grass); one specimen, 18 July 1971; 2 specimens, 27 August 1971, site 17 (grass); one specimen, 17 July 1971; one specimen, 17 August 1971, site 18 (*Coleogyne*).

*Eleodes porcata* Csy.: one specimen, 8 August 1973, site 39 (*Ephedra*-grass).

*Embaphion glabrum* Blais.: 3 specimens were taken at site 1, 3 at site 2, 6 at site 3, 2 at site 19, 4 at site 22, one at site 23, 17 at site 27, and 14 at site 28. Greatest numbers were found at sites 27 and 28. Beetles were taken in July and August of 1971, April to September of 1972, and May, July, and August of 1973. During July and August about equal numbers were found in each of the three years. For the period of May to August, twice as many beetles were taken in 1972 as in 1973.

*Exchatomoxys tanneri* Sorenson and Stones: one specimen, 15 August 1971, site 3 (*Ephedra*-grass).

*Glyptasida sordida* (Lec.): one specimen, 13 August 1971; one specimen, 17 August 1972, site 13 (*Grayia-Ephedra*-grass); one specimen, 12 August 1971; one specimen, 16 July 1972, site 14 (*Coleogyne-Grayia-Ephedra*-grass); 3 specimens, 13-14 August 1972, site 19 (*Coleogyne*); 24 specimens, July and August 1972, site 20 (grass).

*Glyptasida* sp.: one specimen, 15 August 1971, site 3 (*Ephedra*-grass).

*Hylocrinus delicatulus* Csy.: 6 specimens were taken at site 1, 2 at site 14, 9 at site 19, 2 at site 20, and 18 at site 22. Most specimens were found at sites 19 and 22, which are *Coleogyne* communities. Beetles were taken from June to August in 1972, and May to August in 1973. None were found in 1971. In 1972, highest numbers were taken in July, but populations were not significantly different between months in 1973. About twice as many beetles were taken in 1972 as in 1973.

*Metaponium* sp.: one specimen, 17 July 1972, site 14 (*Coleogyne-Grayia-Ephedra*-grass).

*Pelecyphorus haruspex* Csy.: 2 specimens, 28 August 1971, site 1 (*Ephedra-Vanclevea*-grass); 2 specimens, 6 August 1972; one specimen, 6 September 1971, site 2 (juniper-*Ephedra*-grass); 4 specimens, 14 August 1971; one specimen, 25 August 1971; one specimen, 1 August 1973, site 3 (*Ephedra*-grass); 5 specimens, 18, 20 August 1971; 7 specimens, 11-12 August 1972, site 10 (*Ephedra*-grass); one specimen, 28 August 1971, site 18 (*Coleogyne*).

*Sphaeriontis muricata* Lec.: 65 beetles were taken from 11 study sites. They were most abundant on sites 10 (*Ephedra*-grass), 19, and 22 (*Coleogyne*). Specimens were taken in July and August of 1971, May to September of 1972, and in May, June, and August of 1973. Greatest numbers in 1972 were found in July, but in 1971 and 1973 the populations were about equal each month. In July and August twice as many beetles were taken in 1972 as in 1971, and five times as many as in 1973. From May to August four times as many beetles were taken in 1972 as in 1973.

*Steriphanus* sp.: one specimen, 7 April 1972, site 3 (*Ephedra*-grass).

*Triorophus lariversi* Blais.: one specimen, 14 August 1971, site 2 (juniper-*Ephedra*-grass).

*Triorophus tenebratulus* Csy.: 77 beetles were taken from 10 sites, most abundantly from site 22, a *Coleogyne* community. Only two specimens were found in August 1971; most were taken from April to August in 1972, and May to August in 1973. In 1972 and 1973, greatest numbers were found in May. From May to August, only a few more specimens were taken in 1972 than in 1973.

*Trogloderus tuberculatus* Blais: Beetles of this species were the most abundant and widespread of all species collected. A total of

510 specimens was taken from all 19 study sites. Greatest numbers were found on site 19, a *Coleogyne* community. Specimens were found every month that field studies were conducted. In 1971, greatest numbers were found in July, and in 1972 and 1973 in June. In July and August, from two and one-half to three times as many beetles were taken in 1972 as in either 1971 or 1973. From May to August, half again as many beetles were taken in 1972 as in 1973.

## DISCUSSION

An initial objective was to select study areas in the major vegetative types within a 48-km perimeter of the proposed sites of the electric generating stations. Retention of study plots beyond the first year was based on vegetative type, direction from the potential source of pollution, and especially the species and relative abundance of organisms present that could be used as indicator species to monitor environmental changes. Some sites were discontinued after one season because of inaccessibility, discontinuous vegetative analyses, and specific climatic and edaphic data.

In order to compare populations and seasonal changes, the numbers of beetles collected were adjusted to the number of trapping attempts. The normal variability in seasonal and annual populations, slightly different dates of collection each month, and the influence of periodic and abrupt climatic changes on the activity of the beetles during the trapping periods were ignored. Nevertheless, the method used adequately determined relative abundance and distribution within the limitations of time, economy, and logistics. The number of trapping attempts is shown in Table 1.

Pit traps are effective primarily for ground-dwelling arthropods that move on the ground more frequently than they fly. The traps involve minimum effort and time and can be used effectively for those species which may be so trapped. In this study about half of the beetles caught were in the families Carabidae and Tenebrionidae, whose members are primarily ground-dwellers. Nineteen of the species collected were sufficiently abundant to be used as indicators, and 14 of these belonged to the Tenebrionidae, the darkling beetles (Table 2).

Highest populations of beetles of all species occurred in August 1971, July 1972, and June 1973 (Table 3). These annual differences likely are related to climatic and vegetational variations, and when such data are available, multiple regression analyses may show specific correlations.

TABLE 1. Number of trap-days[1] for pit traps on 16 major study sites, 1971–1973.

| Site | 1971 | 1972 | 1973 | Total |
|---|---|---|---|---|
| 1 | 60 | 120 | 90 | 270 |
| 2 | 60 | 180 | 90 | 330 |
| 3 | 60 | 180 | 90 | 330 |
| 4 | 60 | 120 | * | 180 |
| 6 | 60 | 90 | 90 | 240 |
| 8 | 60 | 90 | 90 | 240 |
| 10 | 30 | 120 | 90 | 240 |
| 13 | 60 | 150 | 90 | 300 |
| 14 | 60 | 150 | 90 | 300 |
| 19 | * | 90 | * | 90 |
| 20 | * | 90 | * | 90 |
| 22 | * | 150 | * | 150 |
| 23 | * | 120 | 90 | 210 |
| 27 | * | 120 | 70 | 190 |
| 28 | * | 120 | 70 | 190 |
| 30 | * | 150 | 90 | 240 |
| Total | 510 | 2,040 | 1,040 | 3,590 |

[1] Number of traps multiplied by number of days operated.
*Not operated during year indicated.

TABLE 2. Numbers and distribution of beetles[1] on 16 major study sites, 1971–1973.

| Species | Total number taken | No. sites where found |
|---|---|---|
| *Trogloderus tuberculatus* | 510 | 16 |
| *Eleodes sulcipennis* | 192 | 12 |
| *Eleodes extricata* | 164 | 14 |
| *Eleodes hispilabris sculptilis* | 105 | 10 |
| *Chilometopon abnorme* | 100 | 8 |
| *Aphodius rubidus* | 89 | 10 |
| *Conotus lanchesteri* | 80 | 7 |
| *Eleodes obscura sulcipennis* | 78 | 7 |
| *Triorophus tenebratulus* | 77 | 9 |
| *Sphaeriontis muricata* | 65 | 11 |
| *Embaphion glabrum* | 50 | 6 |
| *Hylocrinus delicatulus* | 37 | 6 |
| *Saprinus lugens* | 34 | 4 |
| *Glyptasida sordida* | 31 | 4 |
| *Ptinus* sp. | 30 | 5 |
| *Eleodes caudifera* | 26 | 6 |
| *Pelecyphorus haruspex* | 25 | 4 |
| *Cimbocera conspersa* | 24 | 6 |
| *Eleodes omissa pygmaea* | 23 | 4 |

[1] Only those species are included of which more than 20 specimens were taken.

The number of species of beetles which occurred on each study site was not consistent for each of the three years (Table 4). Even between sites with the same predominant species of plants, variations occurred between sites and years. This is expected because the presence, abundance, and vigor of plants, especially annual grasses and forbs, varies from year to year as influenced by the local climate. Comparison of these sites showed some significant differences. Sites 4, 19, and 22, primarily *Coleogyne*, had only one species of darkling beetle in common. Sites 19 and 22 had three additional species in common. Site 4 had two species not found on the other two sites, site 19 had two unique species, and site 22 had one unique species. Sites 14 and 23, which also contain *Coleogyne* as a predominant shrub, had one species in common with the other *Coleogyne* sites.

*Ephedra*-grassland sites 3, 10, and 30 had no species in common. One species was common to sites 10 and 30, one to sites 3 and 30, and one to sites 3 and 10. Three species were unique to site 3, and four to site 10. Comparison of sites 1 and 20 (which also had grass as a predominant component) with sites 3, 10, and 30 showed one species in common, one common to sites 1, 3, and 30, one common to sites 1 and 10, one common to sites 3 and 20, and one species unique to site 20.

*Artemisia* sites 6 and 28 had one species in common, two unique for site 6, and one unique to site 28.

*Grayia*-grass sites 8 and 13 had two species in common, and two unique to site 8.

Juniper woodland sites 2 and 27 had one species in common, two unique to site 2, and one unique to site 27.

Species composition differed during the

TABLE 3. Total number of beetles of all species collected in pit traps at 16 major study sites, 1971–1973.

| Month | No. beetles collected | | | | | |
|---|---|---|---|---|---|---|
| | 1971 | | 1972 | | 1973 | |
| | Actual | Adjusted[1] | Actual | Adjusted[1] | Actual | Adjusted[1] |
| April | ° | | 88 | 141 | ° | |
| May | ° | | 74 | 111 | 192 | 250 |
| June | ° | | 208 | 250 | 121 | 290 |
| July | 83 | 332 | 367 | 367 | 118 | 236 |
| August | 232 | 394 | 239 | 287 | 114 | 228 |
| September | 25 | 200 | 49 | 157 | ° | |

[1] Numbers adjusted to number of trap days.

°Traps not operated.

TABLE 4. Number of species captured in pit traps on 16 major study sites, 1971–1973.

| Site | Predominant vegetation | 1971 | 1972 | 1973 | Total |
|---|---|---|---|---|---|
| 1 | *Ephedra-Vanclevea*-Grass | 9 | 12 | 11 | 18 |
| 2 | *Juniperus-Ephedra*-Grass | 6 | 10 | 12 | 20 |
| 3 | *Ephedra*-Grass | 14 | 11 | 11 | 26 |
| 4 | *Coleogyne* | 7 | 6 | ° | 9 |
| 6 | *Artemisia* | 5 | 8 | 5 | 13 |
| 8 | *Grayia*-Grass | 3 | 4 | 8 | 9 |
| 10 | *Ephedra*-Grass | 6 | 9 | 10 | 15 |
| 13 | *Grayia-Ephedra*-Grass | 7 | 9 | 8 | 15 |
| 14 | *Coleogyne-Grayia-Ephedra*-Grass | 7 | 13 | 15 | 20 |
| 19 | *Coleogyne* | ° | 13 | ° | 13 |
| 20 | Grass | ° | 9 | ° | 9 |
| 22 | *Coleogyne* | ° | 11 | ° | 11 |
| 23 | *Ephedra-Coleogyne-Grayia* | ° | 8 | 9 | 12 |
| 27 | Juniper-Pinyon | ° | 5 | 7 | 10 |
| 28 | *Artemisia*-Grass | ° | 4 | 5 | 7 |
| 30 | *Ephedra*-Grass | ° | 4 | 7 | 10 |

°Not trapped during year indicated.

Table 5. Percentage composition[1] of beetles on 16 major study sites, 1971–73.

| | Species of beetle | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | Aph rub | Chi abn | Con lan | Ele his | Ele ext | Ele obs | Ele sul | Emb gla | Gly sor | Hyl del | Sph mur | Tri ten | Tro tub | Other[2] |
| 1 | | 12 | 19 | | 3 | 3 | 17 | 3 | | 5 | 3 | 6 | 17 | (8) |
| 2 | ° | ° | 28 | | 10 | 13 | 4 | ° | | 5 | ° | | 20 | (10) |
| 3 | 6 | | | ° | 23 | 11 | 16 | ° | | | ° | ° | 11 | (17) |
| 4 | | 17 | | 19 | | 4 | 4 | | | | 4 | 7 | 40 | (2) |
| 6 | 7 | ° | | 11 | ° | 19 | 20 | | | | | | 26 | (6) |
| 8 | 10 | ° | | 18 | ° | 30 | 15 | | | | | | 24 | (2) |
| 10 | 3 | 27 | | 16 | ° | | 3 | | | | 11 | 5 | 24 | (7) |
| 13 | 4 | ° | ° | 6 | 8 | | 36 | | ° | | 4 | 4 | 24 | (5) |
| 14 | 18 | ° | | 5 | 5 | | 27 | | ° | ° | 4 | 11 | 19 | (10) |
| 19 | | | ° | | 18 | 5 | ° | ° | ° | 6 | 5 | | 57 | (4) |
| 20 | 4 | | | ° | 5 | | ° | | 45 | 4 | | | 15 | (4) |
| 22 | ° | | 3 | | 13 | | | ° | | 11 | 6 | 9 | 38 | (3) |
| 23 | | | ° | 8 | 5 | | | ° | | | ° | 9 | 69 | (5) |
| 27 | | | 4 | | | | | 36 | | | 3 | 3 | 25 | (5) |
| 28 | | | | | 4 | | | 52 | | | | | 22 | (4) |
| 30 | 35 | | | 21 | ° | | 15 | | | | | | 9 | (5) |

[1] The nearest whole percentage is listed for those which constitute at least 3 percent of the specimens collected. However, percentage is relative to all species of beetles collected. An asterisk indicates presence in numbers less than 3 percent.

[2] Number in parentheses indicates number of other species present, each one less than 3 percent of the total composition.

three years. Four of the 19 species that occurred in relative abundance in 1972 and 1973 were not present in 1971. One species present in 1971 was not taken the other two years, one was present only in 1972, and another only in 1973.

Relative abundance of individuals differed between years. Two species were more abundant in 1971 than in other years, 12 were most abundant in 1972, 6 were most abundant in 1973, and 2 were about equally abundant in 1972 and 1973. In 1972, *Chilometopon abnorme* was 30 times as abundant, *Embaphion glabrum* 2 times as abundant, *Hylocrinus delicatulus* 2 times as abundant, and *Sphaeriontis muricata* 4 times as abundant as in 1973. In 1973, *Aphodius rubidus* was 24 times as abundant, *Cimbocera conspersa* 4 times as abundant, and *Eleodes caudifera* 8 times as abundant as in 1972. In 1972 and 1973, *Eleodes extricata* was 11 times as abundant as in 1971.

In July and August, *Chilometopon abnorme, Eleodes caudifera, Eleodes hispilabris,* and *Eleodes sulcipennis* were most abundant in 1971. *Eleodes extricata* was more abundant in 1972 and 1973 than in 1971. *Cononotus lanchesteri* and *Embaphion glabrum* were about equally abundant all three years.

# ANTS FROM NORTHERN ARIZONA AND SOUTHERN UTAH

Dorald M. Allred[1] and Arthur C. Cole[2]

Abstract.— Ants of 22 species were collected in can pit-traps from 16 different vegetative associations to determine distribution, seasonal and annual occurrence, and population as bases for monitoring environmental impact. Thirteen species were sufficiently abundant and distributed to qualify as indicator species. *Myrmecocystus mexicanus* was the most widespread ecologically. *Pogonomyrmex occidentalis* was the most abundant species, but second in ecological distribution. The greatest number of species was found in the juniper-*Ephedra*-grass association, and the fewest species in *Ephredra-Coleogyne-Grayia.*

In June 1971, ecological studies were initiated by the Center of Health and Environmental Studies at Brigham Young University to establish baselines to determine the environmental impact of the Navajo Generating Station near Page, Arizona, and the proposed Kaiparowits Generating Station in Kane County in southern Utah.[3] Field studies of arthropods were conducted from July to September in 1971, and from May to August in 1972 and 1973. Of the 12 sites operated in 1971, the 16 in 1972, and the 12 in 1973, some were studied only one year, others two, and some all three years.

The trapping method, study sites, and predominant vegetation on each site are described by Allred and Tanner (1971, Great Basin Nat. 39:89–96). The ants were identified by Arthur C. Cole

## Species Commonly Collected

*Camponotus vicinus* Mayr is common and widespread in the arid and semiarid western United States. Nesting generally beneath stones and logs, it is a strong and highly successful contender for space and food.

One specimen was taken at site 1, 106 at site 2, 27 at site 6, 54 at site 19, 41 at site 27, and 5 at site 28. Largest numbers were taken at site 19, a *Coleogyne* community. Ants were taken from July to September in 1971, most abundantly during the latter two months; April to September in 1972, most abundantly in August; and May to August in 1973, also most abundantly in August. Comparison of July and August collections for the three years showed twice as much activity in 1972 and 1973 than in 1971. For the period of May to August, only slightly more activity was noted in 1972 than in 1973.

*Conomyrma insana* (Buckley), known previously as *Dorymyrmex pyramicus* (Roger), has circular and semicircular crater mounds that are characteristic components of desert and semidesert regions, and the agile workers run rapidly over the soil in great numbers during their diurnal foraging.

One of the most common species of ants collected, 238 specimens were taken from 14 of the 19 sites. Largest numbers were found on site 27, a juniper-pinyon community. Ants were found in July and August of 1971, most abundantly in July; from May to September of 1972, most abundantly in August; and from May to August of 1973, also most abundantly in August. Comparison of July and August for the three years showed about equal numbers of ants in 1971 and 1972, but only one-fifth as many in 1973. For the period of May to August, four times as many ants were taken in 1972 than in 1973.

*Crematogaster depilis* Wheeler forms large colonies beneath stones or in nests marked by irregular craters of soil.

Of the total 192 specimens taken from 11 sites, the largest numbers were found on sites 1 and 2, *Ephedra-Vanclevea*-grass and juniper-*Ephedra*-grass communities, respectively. In 1971, ants were found in July and August, more abundantly in August; in April and from June to August in 1972, most abundantly in July; and in May, June, and August of 1973, most abundantly in May. In July and August of the three years, twice as many ants were taken in 1971 than in 1972, and 18 times as many as in 1973.

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[3] These studies were funded cooperatively by Salt River Project, Arizona Resources Corporation, and Southern California Edison.

*Formica obtusopilosa* Emery nests in dry, sunny areas of rather coarse soil. The large entrance is surrounded by an irregular array of pebbles. Workers forage rapidly over the insolated soil surface.

Forty-one specimens were taken at site 3, an *Ephedra*-grass community, and 18 at site 28, an *Artemisia*-grass community. The apparent absence of this species in other areas is unusual. Ants were taken in 1971 in July and August, predominantly in July; in 1972 from June to September in about equal numbers each month; and in about equal numbers from May to August in 1973. Activity for July and August in 1971 was about equal to the same months of 1972, but about five times greater than in 1973. For the period of May to August, four times as many ants were taken in 1972 than in 1973.

*Formica rufibarbis gnava* Buckley forms rather large colonies in earthen nests generally marked by an irregular crater or mound.

Seventy-one specimens were taken at site 2, a juniper-*Ephedra*-grass community, and 7 specimens at site 3, an *Ephedra*-grass habitat. All but one of the specimens were taken in 1971, mostly during July. Only one specimen was taken in 1973, in May.

*Iridomyrmex pruinosum* (E. Andre) is a successful and common component of the desert and semidesert biota. Although it often constructs small circular or irregular craters of fine soil particles, it frequently nests beneath stones and debris. Workers forage rapidly in files even when the soil surface has a high temperature.

Ants were taken from eight sites. More were taken from site 6, an *Artemisia* community, than from any other site. They were found only in August of 1971, and from June to August in 1972.

*Monomorium minimum* (Buckley) is a minute ant that nests beneath stones and detritus, or in open soil with or without a crater. It forms populous colonies.

Thirty-five specimens were taken from seven sites. Largest numbers were found at site 28, an *Artemisia*-grass community. Ants were taken in August 1971, from May to September in 1972, and only in May of 1973. Most of the specimens in 1972 were taken in July. Thirty-one of the specimens were taken during 1972.

*Myrmecocystus mexicanus* Wesmael builds nests in unshaded soil. Each nest is usually surmounted by a mound bearing a single, large circular entrance of firmly packed coarse sand. The workers are nocturnal foragers.

Ants of this species were some of the most abundant and the most widespread of all those found. A total of 652 was taken from all 19 sites, the numbers not different significantly from one site to another. They were found during each of the summer months that studies were made. Largest numbers were found in August of 1971, in July and August of 1972, and in May and June of 1973. Comparison of July and August for each of the three years showed about equal numbers in 1971 and 1972, but only one-third as many in 1973. For the period of May to August, half again as many ants were taken in 1972 as in 1973.

*Myrmecocystus melliger* Forel constructs its nests in rather loose soil marked by a circular or semicircular crater. These ants run rapidly over the ground during their diurnal foraging, and are a conspicuous though familiar element of desert and semidesert areas.

Seventy-one specimens were taken from 12 sites. No significant difference was noted between the numbers of ants at each of the sites. They were taken in July and August of 1971 in about equal numbers; from June to August of 1972, predominantly in July; and in small numbers in May, July, and August of 1973. Comparison of July and August among the three years showed about equal numbers in 1971 and 1972, but only one-fifth as many in 1973. For the period of May to August, four times as many ants were taken in 1972 as in 1973.

*Pheidole bicarinata paiute* Gregg is a small ant with dimorphic workers that generally nests beneath stones in sand or fine soil. Both majors and minors forage largely for seeds during the cooler daytime hours.

A total of 198 specimens was taken from 12 sites. Numbers were highest at sites 6 and 28, which were *Artemisia* communities. In 1971, ants were taken from July to September, mostly in August; from May to September in 1972, predominantly in September; and only in June and July of 1973, predominantly in June. Comparison of July and August for the three years showed twice as many in 1971 as in 1972, and 25 times as many as in 1973. For the period of May to August twice as many were taken in 1972 as in 1973.

*Pheidole sitarches soritis* Wheeler is another dimorphic harvester that constructs small, circular crater nests or sometimes lives beneath stones in unshaded areas.

A total of 110 specimens was taken from 10 sites. Largest numbers were found at site 3, an *Ephedra*-grass community. In 1971 they were found in July and August, mostly July; from June to August in 1972, predominantly in August, and from June to August in 1973, predominantly in June. Comparison of July and August for the three years showed only two-thirds as many in 1972 as in 1971, and only one-fourth as many in 1973. For the period of May to August, numbers were about equal in 1972 and 1973.

*Pogonomyrmex occidentalis* (Cresson) is a common harvester whose numerous, large, conical or subconical mounds, each surrounded by an area cleared of plants, are some of the most conspicuous features of the desert. The nests are usually in coarse, gravelly soil, and both the underground portion and the superstructure contain chambers and galleries in which brood is raised and seeds are stored.

Ants of this species were the most abundant but not the most widespread of all taken. A total of 800 specimens was taken from 15 of the 19 sites. Ants of the species *Myrmecocystus mexicanus* were more widespread than *P. occidentalis*, but not as abundant. This species was most abundant on site 23, although sites 8, 13, and 14 also had relatively high populations. They were found during each of the summer months that field studies were made. In 1971 and 1972 largest numbers were found in August, and in 1973 in June. Comparison of July and August showed four times as many in 1972 as in 1971, and 13 times as many as in 1973. For the period of May to August, eight times as many were taken in 1972 as in 1973.

*Pogonomyrmex rugosus* Emery, another large harvester species, constructs nests surmounted by a low gravel mound or disc with a large, irregular central entrance. The workers vigorously defend their nests and sting readily.

Thirty-three specimens were taken from five sites. Largest numbers were found at site 20, a grass community. Only one was taken in 1971 in July, and the balance in about equal numbers from July to September in 1972.

### SPECIES RARELY COLLECTED

*Camponotus semitestacea* Emery: one specimen 6 June 1972, 3 on 6 July 1972, 3 on 5 August 1972, one on 30 April 1973, site 2—juniper-*Ephedra*-grass; 3 on 4 July 1973, site 6—*Artemisia.*

*Conomyrma bicolor* (Wheeler): 5 specimens 15 August 1972, site 19—*Coleogyne.*

*Crematogaster mormonum* Emery: 7 specimens on 18, 19 August 1971, site 9—*Atriplex Artemisia.*

*Liometopum luctuosum* Wheeler: 2 specimens 19 June 1972, site 28—*Artemisia* grass; 12 on 12 May 1973; 15 on 1 July 1973, site 27—juniper-pinyon

*Myrmecocystus mimicus* Wheeler: 7 specimens on 14, 16 August 1971, site 2—juniper-*Ephedra*-grass; one on 6 June 1972, site 3—*Ephedra*-grass; one on 14 August 1972, site 22—*Coleogyne.*

*Pogonomyrmex imberbiculus* Wheeler: 3 specimens on 18, 20 August 1971, 2 on 11 August 1972, site 9—*Atriplex-Artemisia.*

*Pogonomyrmex subnitidus* Emery: 4 specimens 18–20 August 1971, one on 10 April 1972, 2 on 12 July 1972, 3 on 10, 12 August 1972, one on 11 September 1972, site 10—*Ephedra*-grass.

*Veromessor lobognathus* (Andrews): one specimen 19 August 1971, 2 on 10, 11 August 1972, 2 on 11 September 1972, 6 on 6, 7 June 1973, site 10—*Ephedra*-grass; one on 7 July 1972, site 4—*Coleogyne*; 3 on 12 July 1972, site 8—*Grayia*-grass.

## DISCUSSION

These studies were established in major vegetative types within a 48-km perimeter of the proposed sites of the electric generating stations. Retention of study sites beyond the first year was based on vegetative type, direction from the potential source of pollution, and especially the species and relative abundance of organisms present that could be used as indicator species to monitor environmental changes. Some sites were discontinued after one season because of inaccessibility, discontinuous vegetative analysis, and no specific climatic and edaphic data.

In order to compare populations and seasonal changes, the numbers of ants collected were adjusted to the number of trapping attempts. The normal variability in seasonal and annual populations, slightly different trapping periods within the same month, and the influence of periodic and abrupt climatic changes on the activity of the ants during a given trapping period were ignored.

Pit traps are effective primarily for ground-dwelling arthropods that move on the ground more frequently than they fly. The traps involve minimum effort and time, can be used effectively for those species which may be so trapped, and adequately determine relative abundance and distribution within the limitations of time, economy, and logistics. The number of trapping attempts is shown in Table 1.

Thirteen of the 22 species found in this study are sufficiently abundant and distributed that they may be used as indicator species to determine environmental changes (Table 2).

In this study relative numbers of individuals are referred to as "activity," inasmuch as populations were measured only by above-ground activity and not numbers of colonies or individuals within those colonies. An assumption is made that above-ground activity and abundance is directly proportional to the number of colonies and individuals.

Greatest activity of the ants occurred in July and August of 1971 and 1972, and in June of 1973 (Table 3).

The total number of species varied only slightly during the three years (Table 4). Some study sites showed significant variations where data were available for all three years. On 6 of 8 such sites, a decrease in the number of species was noted in 1973. Where only two years' data were available for 5 sites, one site increased in number of species in 1972 over 1971, 3 decreased in 1973 over 1972, and one was equal for 1972 and 1973. Nine of 12 sites showed a species decrease in 1973 over one or both the two previous years.

Table 5 shows the variety of predominant ants for each of the study sites. *Myrmeco-*

TABLE 1. Number of trap-days[1] for pit traps on 16 major study sites, 1971–1973.

| Site | 1971 | 1972 | 1973 | Total |
|---|---|---|---|---|
| 1 | 60 | 120 | 90 | 270 |
| 2 | 60 | 180 | 90 | 330 |
| 3 | 60 | 180 | 90 | 330 |
| 4 | 60 | 120 | ° | 180 |
| 6 | 60 | 90 | 90 | 240 |
| 8 | 60 | 90 | 90 | 240 |
| 10 | 60 | 120 | 90 | 240 |
| 13 | 60 | 150 | 90 | 300 |
| 14 | 60 | 150 | 90 | 300 |
| 19 | ° | 90 | ° | 90 |
| 20 | ° | 90 | ° | 90 |
| 22 | ° | 150 | ° | 150 |
| 23 | ° | 120 | 90 | 210 |
| 27 | ° | 120 | 70 | 190 |
| 28 | ° | 120 | 70 | 190 |
| 30 | ° | 150 | 90 | 240 |
| Total | 510 | 2,040 | 1,040 | 3,590 |

[1] Number of traps multiplied by number of days operated.

°Not operated during year indicated.

TABLE 2. Numbers and distribution of ants[1] on 16 major study sites, 1971–1973.

| Species | Total number taken | No. sites where found |
|---|---|---|
| *Pogonomyrmex occidentalis* | 800 | 14 |
| *Myrmecocystus mexicanus* | 652 | 16 |
| *Conomyrma insana* | 238 | 12 |
| *Camponotus vicinus* | 234 | 6 |
| *Pheidole paiute* | 198 | 10 |
| *Crematogaster depilis* | 192 | 10 |
| *Pheidole sitarches* | 110 | 9 |
| *Formica rufibarbis* | 78 | 2 |
| *Myrmecocystus melliger* | 71 | 11 |
| *Formica obtusopilosa* | 61 | 2 |
| *Monomorium minimum* | 35 | 7 |
| *Pogonomyrmex rugosus* | 33 | 4 |
| *Iridomyrmex pruinosum* | 26 | 7 |

[1] Only those species are included of which more than 20 specimens were taken.

TABLE 3. Total number of ants of all species collected in pit traps at 16 major study sites, 1971–1973.

| Month | No. ants collected | | | | | |
|---|---|---|---|---|---|---|
| | 1971 | | 1972 | | 1973 | |
| | Actual | Adjusted[1] | Actual | Adjusted[1] | Actual | Adjusted[1] |
| April | * | | 34 | 54 | * | |
| May | * | | 46 | 69 | 116 | 151 |
| June | * | | 266 | 319 | 111 | 266 |
| July | 184 | 736 | 649 | 649 | 88 | 176 |
| August | 424 | 721 | 701 | 841 | 76 | 152 |
| September | 27 | 216 | 96 | 307 | * | |

[1] Numbers adjusted to number of trap days.

*Traps not operated.

TABLE 4. Number of species of ants captured in pit traps on 16 major study sites, 1971–1973.

| Site | Predominant vegetation | 1971 | 1972 | 1973 | Total |
|---|---|---|---|---|---|
| 1 | *Ephedra-Vanclevea*-Grass | 7 | 8 | 8 | 10 |
| 2 | Juniper-*Ephedra*-Grass | 10 | 9 | 10 | 13 |
| 3 | *Ephedra*-Grass | 7 | 9 | 4 | 11 |
| 4 | *Coleogyne* | 4 | 7 | * | 7 |
| 6 | *Artemisia* | 7 | 6 | 3 | 8 |
| 8 | *Grayia*-Grass | 5 | 5 | 3 | 6 |
| 10 | *Ephedra*-Grass | 5 | 8 | 4 | 8 |
| 13 | *Grayia-Ephedra*-Grass | 5 | 7 | 4 | 7 |
| 14 | *Coleogyne-Grayia-Ephedra*-Grass | 4 | 7 | 4 | 7 |
| 19 | *Coleogyne* | * | 9 | * | 9 |
| 20 | Grass | * | 5 | * | 5 |
| 22 | *Coleogyne* | * | 7 | * | 7 |
| 23 | *Ephedra-Coleogyne-Grayia* | * | 3 | 3 | 3 |
| 27 | Juniper-Pinyon | * | 8 | 6 | 9 |
| 28 | *Artemisia*-Grass | * | 8 | 4 | 9 |
| 30 | *Ephedra*-Grass | * | 6 | 2 | 6 |
| | Total | 20 | 20 | 16 | 24 |

*Not trapped during year indicated.

TABLE 5. Percentage composition[1] of ants on 16 major study sites, 1971–1973.

| Site | Species of ant | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Cam vic | Con ins | Cre dep | For obt | For gna | Mon min | Myr mex | Myr pla | Phe pai | Phe sor | Pog occ | Pog rug | Other[2] |
| 1 | * | * | 26 | | | * | 28 | * | 18 | * | * | | (1) |
| 2 | 26 | * | 12 | | 18 | | 20 | * | * | * | * | | (3) |
| 3 | | | 14 | 16 | * | * | 10 | * | 14 | 20 | 17 | * | (1) |
| 4 | | | * | | | * | 41 | * | | * | 38 | | (1) |
| 6 | 19 | | | | | | 26 | * | 36 | | * | | (3) |
| 8 | | * | * | | | * | 23 | | | | 64 | | (1) |
| 10 | | * | | | | | 51 | * | | * | 22 | | (3) |
| 13 | | * | * | | | | 14 | | * | * | 69 | | (1) |
| 14 | | * | * | | | | 24 | * | * | | 63 | | (1) |
| 19 | 55 | * | * | | | * | 16 | * | * | | | * | |
| 20 | | 27 | | | | | * | * | * | | | 49 | |
| 22 | | * | | | | | 53 | * | 27 | | * | * | (1) |
| 23 | | | * | | | | 27 | | | | 72 | | |
| 27 | 15 | 34 | | | | | 24 | * | * | | 11 | | (3) |
| 28 | * | 15 | | 16 | | 19 | * | | 28 | * | * | | (1) |
| 30 | | 21 | * | | | * | 29 | | | * | 43 | | |

[1] The nearest whole percentage is listed for those which constitute at least 10 percent of the specimens collected. However, percentage is relative to all species of ants collected. An asterisk indicates presence in numbers less than 10 percent.

[2] Number in parentheses indicates number of other species present, each one less than 10 percent of the total composition.

*cystus mexicanus* was on all 16 of the sites evaluated, but not significantly abundant on 2 sites. *Pogonomyrmex occidentalis* was on 14 of the sites, but of significant composition on only 9. Only 2 sites had the same species composition (sites 8 and 30), but the relative percentages of each species differed between them.

Comparison of sites which were most alike in predominant plant species showed some significant differences. *Coleogyne* sites 4, 19, and 22 had only one species of ant in common. Site 4 had three unique species, and site 22 had two unique species. Comparison of sites 14 and 23, which also contained significant amounts of *Coleogyne*, showed both sites with one species common to each and to the other *Coleogyne* sites, both sites with two species common to each and to site 4, and site 14 with one species common to site 22.

Comparison of *Ephedra*-grassland sites 3, 10, and 30 showed only one species common to all three. One species was common to sites 3 and 30, one species to 10 and 30, three species unique to site 3, two to site 10, and one to site 30. Comparison of sites 1 and 20, which also had significant amounts of *Ephedra* and grass, showed one species common to each and to sites 10 and 30, one species common to each and to site 3, one common to each and site 30, site 1 with one species common to sites 3 and 30, and with each site with one unique species.

*Artemisia* sites 6 and 28 had only one species in common. Three species were unique to site 6, and four species to site 28.

*Grayia*-grass sites 8 and 13 had three species in common, and each had one unique species.

Juniper woodland sites 2 and 27 had three species in common, site 2 had two unique species, and site 27 one unique species.

Annual differences in species composition varied between the three years. Two species that were active in 1972 and 1973 were not taken in 1971. One species active in 1973 was not taken in the other years, and one species present in 1972 was not taken in the other years. Three species present in 1971 were not taken in 1972 or 1973. One species taken in 1971 and 1973 was not found in 1972, and five species taken in 1971 and 1972 were not taken in 1973.

Relative activity (measured by the number of specimens caught in traps) of individual species differed between years. One species was more active in 1971 than in other years, 10 were most active in 1972, 2 in 1973, and one more active in 1972 and 1973 than in 1971. In years when comparisons could be made for similar months, most species were much more active in 1972 than in 1973. *Camponotus vicinus* was only slightly more active; *Conomyrma insana*, *Formica obtusopilosa*, and *Myrmecocystus melliger* were 4 times as active; *Crematogaster depilis* 3 times as active; *Pheidole paiute* 2 times as active; *Myrmecocystus mexicanus* half again as active; *Pogonomyrmex occidentalis* 8 times as active; and *Monomorium minimum* 33 times as active in 1972 as in 1973. *Pheidole soritis* was about equally active in 1972 and 1973, and *Veromessor lobognathus* was 2 times as active in 1973 as in 1972.

Comparison of the months July and August for the three years showed that *Crematogaster depilis*, *Pheidole paiute*, and *Pheidole soritis* were most active in 1971; *Iridomyrmex pruinosum*, *Monomorium minimum*, *Pogonomyrmex occidentalis*, *P. rugosus*, and *Veromessor lobognathus* in 1972; *Conomyrma insana*, *Formica obtusopilosa*, *Myrmecocystus mexicanus*, *M. placodops*, and *Pogonomyrmex subnitidus* in 1971 and 1972; and *Camponotus vicinus* in 1972 and 1973.

# TABLE OF CONTENTS

Phlox longifolia Nutt. (Polemoniaceae) complex of North America. Frederick J. Peabody ..... 1

Diatom floristics and succession in a peat bog near Lily Lake, Summit County, Utah. Shobha A. Jatkar, Samuel R. Rushforth, and Jack D. Brotherson ..... 15

Vegetational response to three environmental gradients in the salt playa near Goshen, Utah County, Utah. Michael G. Skougard and Jack D. Brotherson ..... 44

Distribution of sculpins in the Clearwater River Basin, Idaho. O. Eugene Maughan and Gary E. Saul ..... 59

Phytoseiid predators of mite pests in Utah apple orchards. Clive D. Jorgensen and Vichitra Mongkolprasith ..... 63

Subspecies specificity of gall forms on *Chrysothamnus nauseosus*. E. Durant McArthur, Charles F. Tiernan, and Bruce L. Welch ..... 81

Homing by a pigmy rabbit. Jeffrey S. Green and Jerran T. Flinders ..... 88

Beetles from the environs of Lake Powell in southern Utah and northern Arizona. Dorald M. Allred and Vasco M. Tanner ..... 89

Ants from northern Arizona and southern Utah. Dorald M. Allred and Arthur C. Cole ..... 97

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8-79 650 40666

ISSN 0017-3614

The Great Basin Naturalist
Published at Provo, Utah, by
Brigham Young University

ISSN 0017-3614

Volume 39 June 30, 1979 No. 2

# REVIEW OF TULAREMIA IN UTAH AND THE GREAT BASIN

Harold E. Stark[1]

Abstract.— This is a compilation of tularemia research conducted in Utah, particularly at U.S. Army Dugway Proving Ground (DPG), Utah, and an evaluation of this information in relation to the current status of tularemia studies. A brief history of tularemia in Utah and a review of field and laboratory studies are included.

Human cases of tularemia occur throughout Utah during all seasons of the year. An analysis of recent human disease reveals a concentration of cases in rural areas, with a greater seasonal occurrence in late summer and early fall.

Research on tularemia as a zoonotic infection in and around the U.S. Army Dugway Proving Ground (DPG), Utah, has established the existence of natural foci of infection, cycles of activity, and probable reservoir hosts and vectors. In addition, studies have been directed toward determination of survival times of the organism as aerosols and as contaminants on surfaces in the laboratory and in nature under varying field conditions. Field and laboratory work also have been conducted at Brigham Young University and the University of Utah; several species of deer fly (*Chrysops* spp.) were found infected in nature.

Human tularemia is commonly a rural disease, probably with an eight-year cyclic tendency in Utah. It is transmissible to man through direct contact with the host, contamination of water and food, vectors, inhalation of dust as from tick feces while shearing sheep, and, uniquely in the Great Basin, by the bite of deer flies.

There have been several review articles on tularemia in recent years; Jellison and Parker (1945), Bell (1965), Olsuf'yev and Rodnev (1960), Hopla (1974), and Olsen (1975) are examples. In addition, several bibliographies have been compiled, e.g.: the U.S. Army Chemical Corps (1958), Hoogstraal et al. (1970–1972), and Pollitzer (1967). Cox (1964), at Brigham Young University, prepared a "Bibliography of Tularemia" with references arranged by subject matter, similar to the one published by the U.S. Army Chemical Corps. Jellison was author (1950) and coauthor (1945, 1951, 1956), of specific and general articles on tularemia (many of them on tularemia in Utah), and he prepared a current review and bibliography on tularemia (1974).

Much of the information given here is a review of large quantities of data from DPG reports and records not ordinarily available to the scientific community. Since the data are voluminous, not all can be analyzed; many DPG reports and articles are referenced for further analysis (if desired) by the reader. Other portions of this work constitute a literature survey.

---

[1] Environmental and Ecology Branch, U.S. Army Dugway Proving Ground, Dugway, Utah 84022.

## HISTORY

The etiologic agent of tularemia, *Francisella tularensis*, was not identified until this century (McCoy 1911, McCoy and Chapin 1912). However, tularemia may have appared earlier among humans in rural Utah. Pearse (1911), a Brigham City physician, studied six human cases of an unknown disease which occurred in August 1908 in the Brigham City-Tremonton area. It is believed to be the first clinical description of tularemia in the English language. Pearse left the disease unnamed. Later medical accounts reviewing epidemiologic and clinical aspects of the disease assumed deer fly bites were associated with it, although no infected insects were captured or identified.

Francis, another physician, first isolated *F. tularensis* from wild mammals and their ectoparasites in 1919 and conducted detailed studies near Holden in the Delta area of Millard County (Francis 1921, 1927). Before 1920 he referred to the disease as "Pahvant Valley plague" and "deer fly fever." Later (1921) he established and used the name tularemia for the disease. Simpson (1929) wrote a textbook on medical aspects of the disease, assembling knowledge to that time. He associated the cases in Utah largely with deer fly bites.

## ETIOLOGIC AGENT

*Francisella* is distinctive and only distantly related to other bacterial organisms. Buchanan and Gibbons (1974) gave no hierarchical arrangement for it. The genus is placed with *Brucella*, to which it is not closely related,[2] in a group of genera of uncertain affiliation entitled "Gram-negative aerobic rods and cocci." There has been no general compilation of strains published to date, although there are significant differences in levels of virulence among strains of *F. tularensis*. Yet virulence alone does not provide a basis for classification, because under laboratory culture and storage it can change. Different laboratory hosts express different levels of resistance and display varying pathogenesis. Biochemical reactions (glycerine fermentation and the presence or absence of citrulline ureidase) have been related to virulence (Marchette and Nicholes 1961). Some strains resist streptomycin. Eigelsbach, Braun, and Herring (1951), Skrodsky (1966), and Dominowska (1967) observed a correlation between the colonial morphology and the pathogenicity and immunogenic properties of a given isolate.

Based on virulence, chemical reactions, morphology, geographic origin, epizootiology, epidemiology, vectors, reservoirs, association of different habitats, and modes of transmission, two basic subspecies of tularemia have gained recognition. These are commonly referred to as types A and B (Bell 1965). Subspecific designations also have been made referring to types A and B. The less virulent of the two is *palaearctica* (Type B) and is more frequently associated with agricultural areas and lotic waters, and may be maintained by chronic tularemia nephritis in muskrats, beavers, and voles. Voles may be the primary reservoir in some areas in western North America. Chronically infected vertebrates urinate onto watersheds, sometimes causing widespread and protracted human epidemics (Bell and Stewart 1975).

Human infection with *palaearctica* has occurred during threshing operations in the USSR. Possible similar occurrence of human tularemia in the Great Basin is discussed later under tularemia in soils. Another proposed name, *holarctica*, for Type B, implies that this type occurrs throughout all land masses of the Northern Hemisphere. Though *holarctica* is less restrictive in concept, *palaearctica* has taxonomic priority. *Francisella t. tularensis* (Type A, also designated *F. t. nearctica*) is more virulent and is frequently associated with infection in lagomorphs (hares and rabbits) and nonaquatic (xeric or mesic) rodents, more frequently involves human cases contracted during hunting, and is often associated with vectorborne transmission than is *palaearctica* (Bell 1965).

Besides the currently recognized subspecies, two additional nomenclatural designations have been proposed, *japonica* (Rodianova 1967) (for Japanese isolates) and *mediasiatica* (Aikimbaev 1966) (for a central Asian strain). Aikimbaev (1966) and Olsul'yev (1970) regard the latter as primitive. Aikimbaev proposed subspecific status for *mediasiatica*. Taxonomic status has not been evaluated for either of these two names.

---

[2] There is some serologic cross reaction between *F. tularensis* and *Brucella* (Hopla 1974, Quan 1978).

The tularemia organism in nature is ubiquitous, but simultaneously demonstrates ubiety with regard to strain differentiation. Numerous strains have been recognized. These often have been designated with numbers or initials. At DPG, nine strains are maintained and studied: Jap 4, Ohara, Live Vaccine, S. C., Russ, Max, 38, 38A, and Schu 5. Similar groups have been kept at several educational institutions, the U.S. Public Health Service, Rocky Mountain Laboratory at Hamilton, Montana; Centers for Disease Control at Fort Collins, Colorado, and Atlanta, Georgia; and at several state health departments. Several strains may occur in one locality (e.g., Prince George County, Virginia, where several strains came from a single species of tick—*Haemaphysalis leporispalustris*). Karlsson et al. (1970) and Karlsson and Soderlind (1973) obtained 50 strains from a limited area in Sweden; most of these came from a single species of tick. Many publications list strains collected locally from nature or developed in the laboratory. In Stoenner et al. (1959) and Marchette and Nicholes (1961), the strains DPG-1,2,3,4,5,6, SKV-1,2,3, and 9-K-161 are reported as isolates from ticks (*Dermacentor parumpertus*, *Hemaphysalis leporispalustris*, and others), cottontails (*Sylvilagus audobonii*), and jackrabbits (*Lepus californicus*) around DPG. Marchette et al. (1961) listed 18 cultures kept at DPG and at the University of Utah, Salt Lake City. A staff report on tularemia at DPG (No. 88U; USA-DPG 1962b) listed 26 strains (18 from DPG) used in susceptibility and vector studies of transmission. There is no record of preservation of these isolates. Some strains are preserved in adjacent states. Dr. Thomas J. Quan of the Plague Branch of the Communicable Disease Center, Fort Collins, Colorado, has strains SKV-2 and DPG-1 as part of his *F. tularensis* collection. Mr. Scott Stewart, Rocky Mountain Laboratory, Hamilton, Montana, preserves numerous strains by lyophylization, but effort is not devoted to identification and cataloging; it is more convenient to obtain fresh material from nature for ongoing research.

Storage and preservation or cultivation (especially in egg yolk) in the laboratory reduces virulence of the organism (Owen 1970). Green (1943) increased virulence of unnamed strains of *F. tularensis* by passage through cottontail rabbits and hares. On the other hand, he contended that passage through grouse reduced virulence. Owen et al. (1961) failed to enhance the virulence of *F. tularensis* by experimentally passing strains through hosts or ectoparasites. Some strains have considerable vitality for sustaining their characteristics. There are great variations of virulence in strains isolated in nature. Older literature on virulence refers to resistance, susceptibility, and mortality in human infections. No assignment of strains, even as far as types A or B, is possible for these old isolations. No classification or cataloging of *F. tularensis* strains appears possible at the present time. Buchanan and Gibbons (1974) suggested a nomenclature that has had partial acceptance at best. Thus, resolving the status of the number and identity of the strains of *F. tularensis* (other than the two principal types) remains an unresolved problem.

## RESEARCH ON TULAREMIA IN UTAH AND THE GREAT BASIN, 1945–1975

Table 1 summarizes research on tularemia in nature in the Great Basin. These investigations are discussed in the following section. Krinsky (1976) devoted about half of his review of tularemia in tabanid flies (*Chrysops* spp.) to the historical occurrence of tularemia in nature in Utah and to research published by Utah-based authors. Krinsky's high regard for studies of tularemia in Utah prompted an expanded review.

DISTRIBUTION, RESERVOIRS, AND CYCLES IN NATURE.— The occurrence of tularemia in Utah differs from that in other parts of the world. Rodenwaldt et al. (1952) believed *F. tularensis* to be ubiquitous in the Holarctic Realm and to occur in permanent and well-defined epicenters where it is maintained, and from which it may spread. The area from

TABLE 1. Summary of basic research on tularemia in the Great Basin, 1945 to 1975.

| Principal Investigators[1] | Date | Institution[2] | Subject of research |
|---|---|---|---|
| Jellison, Parker | 1945 | RML | Rodents, rabbits, and tularemia; *Sylvilagus* ssp.—basic reservoir and source of human tularemia |
| Jellison | 1950 | RML | Deer fly distribution |
| Jellison, Kohls, Philip | 1951 | RML | Tularemia in sheep |
| Jellison, Kohls | 1956 | RML | Tularemia in muskrats and humans around Utah Lake |
| Rodenwaldt | 1952 | U.S. Navy | Concept of epicenters |
| Woodbury, Parker | 1953 | U of U<br>USA-DPG | Special report on tularemia |
| Woodbury | 1954 | U of U<br>USA-DPG | Tularemia and biotic communities |
| U of U staff | 1955 | USA-DPG | Ecology of tularemia transmission |
| Philip, Bell, Larsen | 1955 | RML | Tularemia in jackrabbits in Nevada |
| Allred, Stagg, Lavender | 1956 | USA-DPG | Transmission by *Dermacentor parumapertus* |
| Stagg, Tanner, Lavender | 1956 | U of U<br>USA-DPG | Experimental infection of native animals |
| Parker, Johnson | 1957 | U of U<br>USA-DPG | Attempted transmission by fleas |
| Vest, Marchette | 1958 | U of U<br>USA-DPG | Transmission from infected carcasses |
| Stoenner, Holdenried | 1959 | RML<br>USA-DPG | Isolates of tularemia from Great Salt Lake Desert area |
| U of U staff | 1961 thru 1969 | U of U<br>USA-DPG | Annual reports of surveillance |
| Parker, Olsen, Dolana | 1970 thru 1972 | EcoDynamics<br>USA-DTC | Annual reports of surveillance |
| E&E staff | 1973 to present | USA-DPG | Annual reports of surveillance |
| Lundgren, Marchette, Nicholes | 1961 | U of U<br>USA-DPG | Immunity of host; virulence of pathogen |
| ditto | 1962 | U of U<br>USA-DPG | Cutaneous allergic reaction |
| Gebhart, Thorpe | 1962 | U of U<br>USA-DPG | Review of literature |

Arkansas to southern Illinois constitutes one major epicenter in North America. Another well-defined epicenter exists in the western part of the continent, of which Utah (especially the Delta area) is a part. Later publications attach no particular significance to these epicenters of tularemia as defined by Rodenwaldt et al. Maximov (1960), however, regarded tularemia as an important natural regulator of rodent hosts and reported that it occurs in favorable foci in the USSR as related by the concept of "landscape epidemiology."

Jellison and Parker (1945) proposed that cottontails (*Sylvilagus* spp.) are basic reservoir hosts responsible for 90 percent of human tularemia in North America.

Several species of deer fly are the principal vectors to man from zoonotic sources (possibly infected hares) in Utah. Throughout the remainder of the world, ticks and sometimes mosquitoes (Rodenwaldt et al. 1952) are the principal vectors to man. Other sources of human tularemia infection include contact with the infected hosts, contaminated water, or aerosols.

Tularemia appears to occur widely in a variety of environments and hosts. Few areas are as ecologically diversified as Utah. Tularemia is widespread from the Great Salt Lake Desert to the Uinta Mountains. It has transmission cycles involving waterborne tularemia, as with muskrat trappers around Utah Lake (Jellison, Kohls, and Philip 1951); air-

| | | | |
|---|---|---|---|
| Thorpe, Marcus, Sidwell | 1962 thru 1967 | U of U<br>USA-DPG | Phagocytosis and other cellular factors relating to resistance |
| Cabelli et al. | 1964 | USA-DPG | Transmission by birds |
| Cox | 1964 | BYU | Bibliography of tularemia |
| Cox | 1965 | BYU | Tularemia in deer flies |
| Thorpe et al. (1965) | 1951 thru 1964 | U of U<br>USA-DPG | Tularemia in wildlife and livestock in Great Salt Lake Desert |
| Thorne | 1966 | USA-DPG | Tularemia in soils at DPG |
| Johnson | 1966 | U of U<br>USA-DPG | Ticks of DPG |
| Vest et al. | 1965 | U of U<br>USA-DPG | Five-year review of tularemia field infections in western Utah |
| Knudsen, Rees, Collett | 1968 | U of U<br>USA-DPG | Tularemia in deer flies in Salt Lake County; trapping tabanids |
| Klock, Fukushima, Olsen | 1973 | UDH<br>USA-DTC | Tularemia epidemic: Delta, Grantsville |
| Olsen | 1975 | EcoDynamics<br>USA-DTC | Review of tularemia |

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[1] See bibliography for complete citation.

[2] Institution abbreviations:

BYU = Brigham Young University, Provo, Utah
DPG = U.S. Army Dugway Proving Ground, Utah
DTC = Deseret Test Center, Fort Douglas, Utah
E&E = Epizoology and Ecology Branch prior to 1972; now Environmental and Ecology Branch, DPG
RML = Rocky Mountain Laboratory, Hamilton, Montana
UDH = Utah State Division of Health
USA = U.S. Army
U of U = University of Utah, Salt Lake City, Utah

borne tick feces as with sheep shearers (Jellison and Kohls 1956); direct contact, as with rabbit hunters; and deer fly bites as with 26 of 170 laborers at Locomotive Springs, Utah (Burnette 1936, Hillman and Morgan 1937). These latter authors reported that laborers removed their shirts while working, that sick jackrabbits were seen in the area, and 13 men were known to have killed jackrabbits or handled dead ones. The locations of initial ulcers of the shoulders and backs of the workmen suggested, however, that jackrabbits were not directly involved as a source of human tularemia.

*Francisella novicida* was isolated and described from Ogden Bay, on the eastern side of the Great Salt Lake (Owen 1974), and has never been reported elsewhere. Thus Utah differs from all other areas of the world by harboring all three recognized taxa of *Francisella*.

Epizootiology of tularemia at DPG.— In 1951 a program was begun to study and analyze plants and animals at DPG and adjacent areas (Woodbury 1956, 1964). Emphases were placed on enumerating enzootic pathogens as well as potential introduction of other pathogens to determine possible vectors and routes of natural dissemination. Most research on tularemia at DPG was conducted under contract. Reports entitled "A Study of the Ecology and Epizoology of the Native Fauna of the Great Salt Lake Desert" (Annual Summaries 1951–1969) were published by the University of Utah (USA-DPG 1951–1969). "Ecology Studies of Western Utah" 1971–1973 were prepared by EcoDynamics Incorporated (Desert Test Center USA-DTC 1971–1973). From 1969 through 1964, special summary reports on tularemia were published as DPG in-house reports. These voluminous reports contain much raw data in tables and graphs. Additional tabulation, study, and synthesis of data are not within the scope of this review. The following provides a cursory summary of some results.

From 1951 through 1979 evidence of tularemia existed in virtually all 46 areas of Utah in which specimens were collected and from 35 areas sampled routinely. Serologic evidence of the organism was found infrequently from rodents, usually in less than 1 percent of the specimens. In contrast, high rates were found for carnivores and livestock, usually greater than 11 percent, while moderate rates were recorded for deer and wild horses. Greater risk of exposure, longer lives, innate resistance, and persistence of antibodies may account for higher occurrence in these mammals as opposed to rodents. The incidence of antibodies was usually similar in widely different groups of hosts in the same year. For example, in 1965 22 percent of 651 cattle samples were positive, 42 percent of 1,579 sheep samples were positive, and 25 percent of 31 carnivore samples were positive. In 1968 the proportions of samples with antibodies to *F. tularensis* were small: 0.03 percent for rodents, 2 percent for livestock, and 3 percent for carnivores. In other years carnivores persisted with high rates, and rates in other animals were low. For example, in 1970 antibody rates were 4 percent in sheep, 0.4 percent in cattle, 0 percent for rodents, and 17 percent for carnivores. Antibody recoveries from rodents and jackrabbits remained consistently small however, suggesting that rodents play a minor role in maintenance. Also of little significance to the maintenance of *F. tularensis* in nature is the jackrabbit, which is very susceptible and succumbs promptly. This observation may explain why few jackrabbits in nature possess antibodies to tularemia.

A special summary report prepared by the Ecology and Epizoology research staff, University of Utah, summarized DPG studies on host relationships for ticks, lice, and fleas (USA-DPG 1962b). The report discussed experimental vector transmission studies that included immunization and susceptibility experiments using several strains of *F. tularensis* on laboratory mice, rabbits, guinea pigs, and deer mice. Isolations from wild mammals, birds, and livestock were tabulated. Ecological observations on biotic communities and population dynamics, particularly for the jackrabbit, were summarized. Serologic methods for detecting antibody activity, especially agglutinating, complement-fixing tests, and cutaneous responses were reviewed. Some of the information in this report has not appeared in published literature.

Stagg, Tanner, and Lavender (1956) produced experimental infection of *F. tularensis* in jackrabbits, seven species of rodents, and coyotes (*Canis latrans*). They found that coyote pups were less susceptible to tularemia than rodents. Infection of rodents via contaminated food was difficult. When infection of rodents and jackrabbits was successful (as from aerosols), the disease usually progressed rapidly to death (3–5 days).

Gebhardt and Thorpe (1962) presented a tabular review of worldwide vectors and hosts. The pathogen, vectors, hosts, epidemiology, epizootiology, and control were given a generalized interpretation. Thorpe et al. (1965) reported on tularemia studies from their inception at DPG (1951 through 1964). Areas of study included the Bonneville Basin of western Utah and adjacent portions of Nevada, where 35 areas were sampled semiannually or quarterly. During the 13-year period 52 isolations of *F. tularensis* were made, approximately half from wild mammal tissues and half from ectoparasites. The authors also tabulated information on human tularemia from 1941 through 1964. This information, updated with data from the Utah State Division of Health, is presented in this article as Figure 1 and is discussed later in the section: "Distribution of Recent Cases of Tularemia in Utah." Isolation data with respect to livestock, wild mammals, birds, and their ectoparasites and collections of positive sera were also tabulated. Six local epizootics were observed during the 13-year period. Tissue isolates were made from jackrabbits, which were collected in great abundance, one cottontail, and four rodents. Serum agglutinins were found in birds, wild mammals (including deer), and livestock (roughly 25 to 30 percent of the serum samples tested). Most isolates possessed maximal virulence; however, two isolates from the cottontail and a Great Basin pocket mouse (*Perognathus parvus*) were of low virulence. Thorpe et al. indicated that strains from North American nonaquatic hosts and ectoparasites are sometimes of lower virulence.

Vest et al. (1965), in a five-year study of enzootic diseases in Utah, reported that 10 strains of *F. tularensis* were isolated from lagomorphs and rodents. All strains were of maximum virulence. One viable organism sufficed for a lethal dose in laboratory rabbits, mice, hamsters, and guinea pigs. Olsen and Dolana ([EcoDynamics, Inc.] USA-DTC 1971–1973) provided additional support to Stagg, Tanner, and Lavender (1956), Marchette et al. (1961), and Thorpe et al. (1965).

Olsen and Dolana found that (1) *F. tularensis* isolated from most hosts near DPG usually had maximal virulence, but occasional isolations had little virulence; (2) carnivores were readily infected but recovered and did not demonstrate a carrier state; (3) cottontails were susceptible to infection; and (4) jackrabbits were more susceptible than cottontails. Klock, Olsen, and Fukushima (1972) obtained eight isolations of *F. tularensis* from *Chrysops discalis*, *Dermacentor parumapertus*, *H. leporispalustris*, and jackrabbits from four areas near DPG (Delta,[3] Iosepa, Callao, and Gold Hill). Tests of virulence showed all eight to be typical Type A (*nearctica*), which is virulent for laboratory mice and rabbits. EcoDynamics personnel ([Olsen and Dolana] Desert Test Center 1971 Annual Report [USA-DTC 1972]) were mystified by the large numbers of seropositive cottontails near Delta because tularemia is uniformly fatal to cottontails. They hypothesized that (1) Delta cottontails were somewhat resistant to *F. tularensis* as a result of selection pressure, or (2) the detection of the antibody was a nonspecific reaction, or (3) an avirulent strain of *F. tularensis* (present in the area) was responsible for the antibody titers. They found support evidence that there probably were specific and protective antibodies for cottontail rabbits in the Delta area. Selected details of these supportive data are given later under "Hosts." On the basis of their findings, the EcoDynamics staff (1972) questioned the validity of the generally accepted concept (based primarily on virulence) of types A and B for *F. tularensis*. Olsen and Dolana conjectured further that neither type is limited to specific habitat types nor to specific animal groups. They stated that types A and B allow synthesizing the bewildering array of strains into an epizootiological pattern. No alternative method for organization or cataloging was offered.

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[3] Delta, 97 air km (60 air miles) from Dugway, is not physically near, but is environmentally similar with few barriers between the two areas.

Olsen (1975) reviewed some of the Great Basin surveys by DPG abstracted in the preceding paragraphs. He noted that the majority of isolations of *F. tularensis* came from jackrabbits and its primary tick parasite (*D. parumapertus*), but agglutinins were detected in 22 percent of blood samples from cattle and sheep. Of interest is the decline in rate of recovery of evidence of the tularemia organism in nature from 1954 to 1970. The majority of isolations were made earlier with comparatively little change in field collecting effort. This suggests wide and long-term variation in the amount of pathogen circulating in native reservoir hosts and vectors of the area.

EPIDEMIOLOGY OF TULAREMIA AROUND DPG.— Klock, Olsen, and Fukushima (1973), who described an outbreak of tularemia in 1971 near Delta and Grantsville, Utah, studied the epidemiology of 39 human cases with investigations of vectors, hosts, and incidence of isolations from specimens collected. Nineteen of these human cases suffered deer fly bites, and another nine reported insect bites by unknown species. The pathogen was isolated from hosts and vectors in both areas and adjacent areas such as Skull Valley, Utah. Also, there was an epizootic among lagomorphs. *F. tularensis* was isolated from tissue of jackrabbits and cottontails. Because of unusually large numbers of midges (*Leptoconops* spp. and *Culicoides* spp.) observed in 1971, the authors suggested that these might have played a role in the human outbreak.

VECTORS.— Cox (1965), in a study on *F. tularensis* and deer flies in the environs of Utah Lake, isolated the organism from *Chrysops* spp. in nature for the first time. Experimental transmissions by *C. discalis* was demonstrated by Francis and Mayne (1921). Cox's isolation of *F. tularensis* from *C. fulvaster* and *C. aestuans* demonstrated that species other than *C. discalis* (this common species was only suspect before that time) are vectors. Knudsen, Rees, and Collett (1968) isolated *F. tularensis* from *C. discalis,* thus associating the bite of *C. discalis* with a human case. Other isolations of *F. tularensis* from deer flies from near the Great Salt Lake, made by the University of Utah Ecology and Epidemiology group, suggested a potential health hazard from *Chrysops* spp. Krinsky (1976) pointed out that isolations from deer flies in Utah in 1965, 1968, and 1969 provided evidence of the potential importance of these tabanids in the dissemination of *F. tularensis*, even though they are regarded as short-term mechanical vectors. After these isolations, EcoDynamics researchers made net collections of tabanids and later suggested epidemiologic associations with human cases (Deseret Test Center Annual Reports, USA-DTC 1971–1973). Klock, Olsen, and Fukushima (1973) suggested the same associations (discussed later in this review). Philip (1968) found that another tabanid (*Tabanus punctifer*, may have been associated with a human case reported near Battle Mountain, Nevada.

Parker (1957) and Parker and Johnson (1957) attempted the transmission of *F. tularensis* by fleas in the laboratory. In one attempt, three species of fleas were infected, but none of them transmitted *F. tularensis* to a susceptible host. In another attempt, *Orchopeas leucopus* transmitted *F. tularensis* to a specimen of *Peromyscus treui.* Extensive studies on transmission of tularemia by ticks, overwintering, and transovarial passage of the pathogen have been conducted at Rocky Mountain Laboratory in Hamilton, Montana (Jellison 1974). Vector studies of tick transmission are reported in the University of Utah Ecology and Epidemiology Annual Report (USA-DPG 1962b). *Otobius lagophilus,* removed from a dead jackrabbit, transmitted *F. tularensis* to cottontails and to a domestic white rabbit (*Oryctolagus* spp.), the first known transmission by this tick. Twenty-two species of ticks were recorded from DPG and environs, of which five species (*Dermacentor andersoni, D. parumpertus, Ixodes kingi, Haemaphysalis leporispalustris,* and *Otobius lagophilus*) were infected with *F. tularensis* (Johnson 1966, Thorpe et al. 1965, and Annual Reports USA-DPG 1962–1969). It is conceivable that, in the Great Basin, the tick and jackrabbit (*D. parumapertus* and *L. californicus,* respectively) constitute a polyhostal reservoir (Hopla 1974:47).

HOSTS.— Marchette et al. (1961) demonstrated the susceptibility of locally captured wild mammals to tularemia. Eleven species of wild rodents and cottontails were very susceptible. Some species of wild rodents (*Onychomys leucogaster, Peromyscus maniculatus,* and *Neotoma* sp.) were very susceptible to virulent strains but were resistant to the avirulent "38" strain. Carnivores (*Taxidea taxus, Vulpes macrotis,* and *Canis latrans*) were readily infected orally; the infection soon was no longer demonstrable, and the animals did not become carriers. The authors concluded that tularemia in the Bonneville Basin is a disease primarily of jackrabbits, with the cycle in nature maintained by that host and the vector (*Dermacentor parumapertus*). The authors also concluded that *Lepus* spp. were more susceptible than *Sylvilagus* or *Oryctolagus.* The published conclusions of these authors differ from the general concept throughout the Annual Reports (USA-DPG 1964–1969) that jackrabbits are so susceptible that they play a minor role in maintenance. The snowshoe hare (*L. americanus*; European counterpart—*L. timidus*) is less susceptible than jackrabbits or Minnesota *Sylvilagus* spp. to infection with *F. tularensis* (Green 1943, Green, Larsen, and Bell 1939). Marchette et al. (1961) noted that *L. c. deserticola* was more susceptible than *L. c. texianus.*

About half of 19 cottontails (*S. audobonii*) captured near Delta showed no demonstrable levels of antibody to *F. tularensis* (EcoDynamics Inc. USA-DTC 1972). However, 9 survived the challenge inoculation of 83 cells of *F. tularensis*; they had developed high levels of antibodies. Subsequently, an isolate from cottontails from Delta was tested on other cottontails collected from Delta and Gold Hill. All of the experimental hosts from Gold Hill died, suggesting that some of the Delta cottontails were naturally "immunized" with an avirulent strain of *F. tularensis.* This natural avirulent strain may have been responsible for previously observed seropositive cottontails (31 percent of 62 specimens) collected near Delta in 1972 (USA-DTC 1972). EcoDynamics concluded that Delta cottontails may possess some innate resistance to certain strains of *F. tularensis.* However, much more work needs to be done to clarify the relation, if any, between lethality of various strains and the response of partially resistant hosts (such as laboratory rats and cottontails).

The EcoDynamics group (USA-DTC 1972) reported that 54 carnivores (41 percent) had significant levels of hemagglutinins for *F. tularensis.* This group of carnivores included 52 bobcats (*Lynx rufus*), 19 badgers (*Taxidea taxus*), 8 skunks (*Mephitis mephitis*), 19 coyotes (*Canis latrans*), 30 kit foxes (*Vulpes macrotis*), and 2 domestic cats (*Felis domesticus*). The positive specimens came from the 13 collecting areas around DPG. A more sensitive hemagglutination technique was developed in the early 1970s. Therefore, the higher percentage of serum samples with agglutinins found from 1970 to 1972 (11 percent), may be expected to have higher (though not significantly higher) values when compared to those calculated from tube agglutination testing from 1960 to 1969 (roughly 8 percent). The two tests (tube agglutination, later replaced by microagglutination, and hemagglutination) are discussed later under "Methodology."

The phenomenon of carnivorism among rodents is well known in literature for both dissemination and maintenance of plague and tularemia. Vest and Marchette (1958) fed carcasses of 119 rodents (*Peromyscus* spp.) infected with *F. tularensis* to 11 species of rodents (squirrels, heteromyids, and cricetids). In all cases, every rodent that ingested infective flesh contracted tularemia. Some species (mostly heteromyids) were reluctant to feed on flesh, but did so when starved. The extent to which wild rodents supplement their natural diet with flesh was not determined.

Cabelli, Ferguson, and McElmury (1964) and Cabelli et al. (1964) reported that the mourning dove (*Zenaidura macruora*) is relatively resistant to *F. tularensis,* but the authors speculated that fecal transmission could be significant in dissemination of tularemia to susceptible birds. It is of interest that, when a Schu strain of *F. tularensis* was administered to several species of oceanic birds by several routes, few transmissions from infected to susceptible birds were observed. *Francisella tularensis,* however, was found in the bird excreta although no other evidence of disease (bacteremia) was noted. The brown noddy (*Anous stolidus*), whitecap noddy (*A. min-*

*utus*), white tern (*Gygis alba*), and sooty tern (*Sterna fuscata*) were susceptible to infection. Infection in these birds was achieved by respiratory or cutaneous pathways, rarely by the oral route.

HOST IMMUNE SYSTEM.— Thorpe and Marcus (1962, 1964a,b, 1965a,b,c, 1966, 1967) and Thorpe, Sidwell, and Marcus (1964) reported on the implication of phagocytosis in *F. tularensis* infections. They determined that the phagocytic system of the immune mechanism functions as importantly as the antibody system for resisting and overcoming infections.

STUDIES OF *F. TULARENSIS* IN SOILS AND ON FOMITES.— At DPG research and testing was conducted on *F. tularensis* to characterize its aerosol stability and persistence in soils and on fomites. Many observations and experiments were conducted by DPG Life Science Division that were apart from studies by contractor groups to DPG such as the University of Utah and EcoDynamics, Inc. and in-house field work by the Environmental and Ecology Branch. Most specific studies on *F. tularensis* were highly specialized and printed as numbered reports (other than USA-DPG 1951–1969, USA-DTC 1971–1973, USA-DPG 1976, 1978, and University of Utah contract reports). The primary purpose of field-related work (referenced above) was to study the nature and geographic distribution of tularemia occurring naturally in the DPG area. An additional purpose was to monitor the potential for intrusion or establishment of tularemia relative to test activities. Both laboratory and field studies of aerosols were conducted from the early 1950s through the late 1960s. Many facts were reported concerning *F. tularensis* in nature. Unfortunately, this information was not readily available to the scientific community at large. Many of these documents are now available through interlibrary loan.

An experiment by Thorne (1966) is pertinent to this presentation. Three predominant soils of the DPG area (sand dune, clay flat, and salt flat) were inoculated with *F. tularensis*. The pH of the three soil types varied but little (7.5–7.9). In general, sand dunes were the least favorable for preservation of *F. tularensis*, probably because this soil dried out faster than the other two. High moisture in the soils at the time of inoculation was the single most important factor for survival. Survival of the organism was better below the surface. Subsequent wetting increased survival. Exposure to sunlight was deleterious. The maximum times after inoculation that tularemia organisms could be recovered from the soil were 90 days in winter and 35 days in summer. When conditions were adverse (as in summer heat), survival was as short as a few hours.

An interesting problem has been reported from USSR by Olsuf'yev and Rodnev (1960). Tularemia infection of humans is acquired by the pulmonary route while harvesting cereal crops. Crops were apparently contaminated by infected *F. t. palearctica*, and human infection resulted from inhalation of dust raised into the air from contaminated straw and grain. These conditions are reported to have caused mass infections in people processing the harvest (Spendlove 1974). Popek et al. (1969) reported that washing sugar beets contaminated by infected rodents in a sugar beet works in South Moravia created aerosols that infected 237 people over four harvesting seasons. To date, similar events have not taken place in the Great Basin. Waterborne tularemia did infect human beings in Oregon during a meadow mouse population explosion (Jellison, Bell, and Owen 1959). A potential for airborne infection of tularemia exists throughout the Great Basin whenever threshing or harvesting operations occur.

## METHODOLOGY

SEROLOGY.— With the basic technique of Alexander, Wright, and Baldwin (1950), the staff of EcoDynamics and their predecessors developed a highly sensitive hemagglutination (HA) test. Dr. Bruce Hudson at the Public Health Service, Center for Disease Control, Fort Collins, Colorado, assisted in preparing lipopolysaccharide extract of *F. tularensis* for sensitizing sheep cells. This method is currently used at DPG. Tube agglutination (TA) was replaced by microagglutination (MA) in 1977. Hemagglutination (HA) was first tried by EcoDynamics in 1970, and this test replaced TA in 1972.

Duplicate samples were tested in 1973 and 1978. According to the 1973 Annual Report

(USA-DPG 1976:89–94 and Table 44), testing by untanned sensitized sheep erythrocytes was more sensitive to the presence of antibodies to *F. tularensis* than was testing by agglutination of a stained antigen (MA) by antibodies in unknown samples. The polysaccharide sensitized sheep cells are more likely to yield false positive tests. Today the more sensitive HA test is used as a screen and second confirmation, and the less sensitive MA test is used as a final confirmatory test. In all replicates MA and TA tests gave similar results and TA has been discontinued.

Recovery of pathogen from infected arthropods.— Improvements in techniques are presented in the 1973 Annual Report (USA-DPG 1976). Though the passive HA micro-test became firmly established, discussions of other methods in earlier Annual Reports (USA-DTC 1971–1973) merely allude to more recently developed methods. One of these is the hemolymph test (Burgdorfer 1970), in which the distal end of a tick leg is cut and the hemolymph collected on a slide, stained with immunofluorescent or other dye, and examined. This method was discussed in some detail in the 1971 Annual Report (Deseret Test Center USA-DTC 1972). However the test has not been used at DPG.

Skin test for evidence of tularemia.— Cutaneous allergic reactions have been developed for the diagnosis of tularemia in rodents and rabbits (Lundgren, Marchette, and Nicholes 1961, 1962). Cutaneous sensitivity was elicited by inoculating as few as 10 *F. tularensis* cells; sensitivity was demonstrable for 25 to 53 weeks, depending on species. This diagnostic test aids in establishing previous infection with tularemia for wildlife species. Buchanan, Brooks, and Brachman (1971) reviewed the use of skin tests for human clinical identification of tularemia and epidemiologic studies. Human reactors may remain hypersensitive for as long as 40 years. Antigen prepared for a human skin test (but suitable for use on hosts such as jackrabbits) is available at the Center for Health and Environmental Studies at Brigham Young University.

Immunofluorescence.— Karlsson et al. (1970) and Karlsson and Soderlind (1973) reviewed the use of immunofluorescent (IF) technique in identifying 54 strains, 4 from man and 50 from natural hosts (mostly hares and ticks) in Sweden. They found that once techniques have been established in a given laboratory, histopathologic examination was simplified, and the hazard of laboratory-acquired infection was reduced. The IF method was successful for identifying tularemia in decomposed material. Cutaneous allergic reactions and IF techniques are two promising methods for identifying current tularemia activity in human and other mammal populations around DPG.

A technique for sampling tabanids for F. tularensis.— Knudsen, Rees, and Collett (1968) described a trap designed to obtain large numbers of deer flies and other tabanids for surveys for the tularemia organism. The trap is pyramidal, about 1 m high and 1 m across the base. About midway up the triangle face on either side is a rectangular flapped opening for flies to enter. Once inside, the flies can enter a funnel (20 cm diameter) against the tip of the pyramid. The top of the funnel is closed but has small openings around the perimeter. Some of the flies inside the funnel may fall through the narrow end, through a plastic tube into a styrofoam box beneath containing 4 to 8 kg of dry ice, which freezes the flies. The sublimation of carbon dioxide also serves as an attractant and is the only bait used. During one season (1968), Knudsen, Rees, and Collett trapped 1,248 deer flies (*C. discalis*) from marshes bordering the southeastern shore of the Great Salt Lake. Isolates of *F. tularensis* were obtained from flies trapped in this manner.

## Recent and Current Projects

During 1974 and 1975 personnel at DPG further improved the hemagglutination test, which had proved valuable for the staff of EcoDynamics. Lipopolysaccharide antigen was prepared for serologic examination of wildlife and livestock serum specimens collected around DPG. The macroagglutination test has been replaced by a microagglutination test in accordance with Massey and Mangiafico (1974). Owen (1974) described morphology and characteristics of *F. tularensis* and provided information useful in growing and identifying isolates.

With these recently improved techniques it has been reconfirmed that low levels of antibody occur in serum samples taken from rodents and lagomorphs and a higher incidence occurs in serum samples from carnivores. As presented in preceding annual reports (USA-DPG 1951–1969), sera from a few wild horses at DPG were nearly all positive, but generally antibody response in livestock varied. A greater percentage of sheep seem to possess tularemia agglutinins after a stay on a distant summer range than sheep bled during the winter around DPG. Curiously, specimens of deer serum contributed by hunters in 1973 possessed no demonstrable antibody, though response in deer had been high during some previous years.

Incidence of tularemia in wildlife around DPG will be reviewed in future publications. The first will deal with jackrabbit population changes and tularemia. There has long been an assumption that population reduction of jackrabbits is somehow associated with outbreaks of tularemia in nature. During the last 13 years quantitative data have been collected around DPG which support the general observation that the jackrabbit is subject to large changes of a cyclic nature. While dying jackrabbits infected with *F. tularensis* have been found, the organism or the disease it produces has not been proved responsible for a widespread decline in jackrabbits. For example, Philip, Bell, and Larsen (1955) recorded infected *Dermacentor parumapertus* from infected jackrabbits during a peak in the population cycle of these lagomorphs in Nevada. Firm evidence that tularemia was responsible for eventual decline of the population was not demonstrable. There appears to be simultaneous association of pathogen activity (e.g., evidence of antibodies) from cattle, sheep, carnivores, cottontail rabbits, jackrabbits, and rodents. There also seems to be an inverse correlation with jackrabbit density, particularly the marked decline of jackrabbits in the DPG area (definitely evident in 1973). At that time there was an apparent increase in tularemia activity. This event followed rather closely the increase of activity of *F. tularensis* in all indicator species during the early 1970s.

Epizootiologic and epidemiologic studies were conducted in California (outside the Great Basin) by Lane and Emmons (1977). They concluded that human cases have gradually decreased since 1927, and they theorize that the cause was urbanization and selective pressures that have resulted in a decreased virulence of organisms maintained by reservoir species. A gradual decrease is not evident from data on human tularemia collected from Utah, but urbanization correlates with a decrease of incidence of tularemia as in California. There is a periodic resurgence in time that may be more marked in Utah than in California.

## Distribution of Recent Human Cases

The Communicable Disease Section of the Utah State Division of Health has kept records of reportable diseases, including tularemia, for many years. With their permission, recent records representing current conditions have been tabulated and are presented as part of Figure 1. Thorpe et al. (1965) and Jellison (1974) have assembled records of tularemia cases through 1964. Jellison's format has been used here with additional detailed information included.

In Figure 1 the number in each county on the upper right is 1 percent of the human population in 1977. The number on the upper left is the total cases of tularemia reported from 1941 through 1977 (37 years). The larger figure in the center of the county is the number of tularemia cases per 100,000 persons per annum, averaged for 37 years. The ratio between the total number of cases in each county and the 1977 population of each county was analyzed with a posteriori test by simultaneous testing of the homogeneity of sets of replicates for goodness of fit (G-Statistic, Sokal and Rohlf 1969). Ten sets of samples (under "maximum nonsignificant ranges" in Table 1) were homogeneous; that is, no ratio within each of these sets was significantly different at the 5 percent level of confidence. The counties which are indicated as significantly higher under "exclusive ranges of homogeneous ranges" overlap with no ratio included in the low group. Ratios in Table 2 are expressed as average cases per 100,000 per annum on the map. Three rural counties, Daggett, Millard, and Rich, had values above 15 per 100,000. Seven more rural

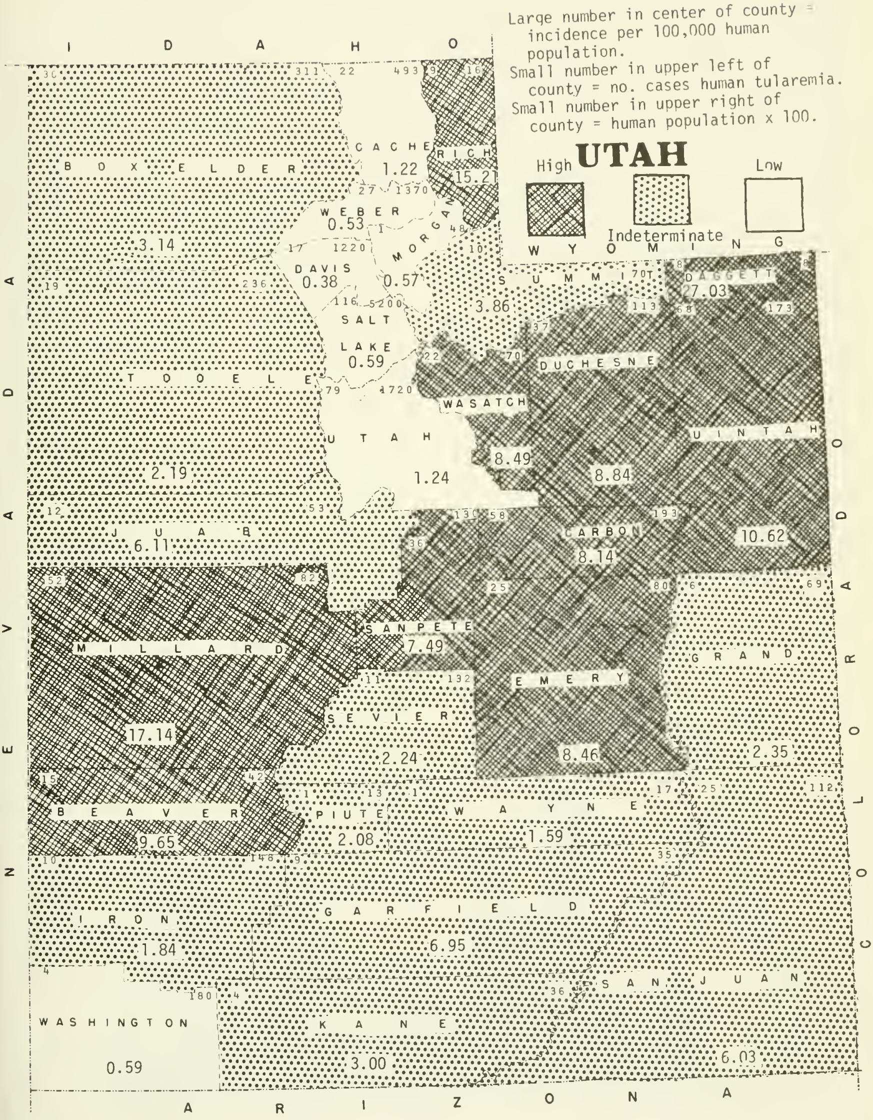
Large number in center of county = incidence per 100,000 human population.
Small number in upper left of county = no. cases human tularemia.
Small number in upper right of county = human population x 100.
UTAH
High
Indeterminate
Low
IDAHO
WYOMING
NEVADA
COLORADO
ARIZONA
BOX ELDER 30 311 3.14
CACHE 22 493 1.22
RICH 9 16 15.21
WEBER 27 1370 0.53
MORGAN 1 48 0.57
DAVIS 17 1220 0.38
SALT LAKE 116 5200 0.59
TOOELE 19 236 2.19
SUMMIT 10 70 3.86
DAGGETT 8 8 7.03
DUCHESNE 37 113 8.49
UINTAH 68 173 10.62
WASATCH 22 70 8.49
UTAH 79 1720 1.24
JUAB 12 53 6.11
CARBON 58 193 8.14
MILLARD 52 82 17.14
SANPETE 36 130 7.49
EMERY 25 80 8.46
GRAND 6 69 2.35
SEVIER 11 132 2.24
BEAVER 15 42 9.65
PIUTE 1 13 2.08
WAYNE 1 17 1.59
SAN JUAN 25 112 6.03
IRON 10 146 1.84
GARFIELD 9 35 6.95
WASHINGTON 4 180 0.59
KANE 4 36 3.00

Fig. 1. Incidence of human tularemia, 1941 through 1977.

counties, Beaver, Carbon, Duchesne, Emery, Sanpete, Uintah, and Wasatch, had values above 7 per 100,000. Counties with the lowest values (less than one per 100,000), Davis, Weber, Morgan, and Salt Lake, are located along the Wasatch Front, which has dense human population (except for Morgan County). Washington County also has a very low value. The average for the entire state of Utah (1941 to 1977) is 1.66 cases per 100,000 per annum.

Figure 2 shows the actual number of known cases in Utah by year from 1960 through 1977. Two periods of increase above average occurred during the years 1961 through 1964 and 1969 through 1971. Values less than 10 were experienced from 1965 through 1968, and the high of 1971 was followed by a series of values which were lowest for the longest departure from the average for 1972 through 1977.

Distribution of cases by month for the 17 years preceding 1978 is shown in Figure 3. These cases represent date of report, not date of onset or contact with sources of infection. In most cases contact would occur about a month earlier, making the lowest three months January through March, and highest three months July through September.

TABLE 2. Homogeneity of sets of replicates tested for goodness of fit.

| County | Ratio: Cases / Pop. | Maximum Nonsignificant Ranges | Exclusive Ranges of Homogeneous Ratios |
|---|---|---|---|
| Daggett | .01000 | | |
| Millard | .00634 | | |
| Rich | .00562 | | |
| Uintah | .00393 | | |
| Beaver | .00357 | | |
| Duchesne | .00327 | | High |
| Wasatch | .00314 | | |
| Emory | .00312 | | |
| Carbon | .00301 | | |
| Sanpete | .00277 | | |
| Garfield | .00257 | | |
| Juab | .00226 | | |
| San Juan | .00223 | | |
| Summit | .00143 | | |
| Box Elder | .00116 | | |
| Kane | .00111 | | |
| Grand | .00087 | | Indeterminate |
| Sevier | .00083 | | |
| Tooele | .00081 | | |
| Piute | .00077 | | |
| Iron | .00068 | | |
| Wayne | .00059 | | |
| Utah | .00046 | | |
| Cache | .00045 | | |
| Salt Lake | .00022 | | |
| Washington | .00022 | | Low |
| Morgan | .00021 | | |
| Weber | .00020 | | |
| Davis | .00014 | | |

## REVIEW AND CONCLUSIONS

Tularemia organisms were probably present in nature and in man around the turn of the century in Utah and perhaps earlier. *Francisella tularensis* in Utah is ubiquitous in terms of habitat. Type B (*F. t. palaearctica*) typically occurs as an aquatic infection and may be transmitted from natural sources (including water and aquatic mammal hosts) to humans and to nonaquatic hosts by ingestion, contact, aerosols, and several arthropod vectors (Jellison, 1974). Type A (*F. t. tularensis*), the more virulent form, which usually occurs in nonaquatic hosts and their arthropod vectors, is more widespread; its distribution overlaps the aquatic type. Human cases have occurred in all counties of Utah. The Delta area has sustained repeated human tularemia infections in which the deer fly has served as a major vector.

Although *F. tularensis* is highly invasive, it is fragile and difficult to cultivate and maintain. Strains of greater and lesser virulence occur in nature, apparently simultaneously at the same site and even in the same host or vector. Despite well-documented strain differentiation, only two subspecific designations are accepted currently. Classification of tularemia organisms is a complicated subject. No coordinated effort by researchers has been made to keep all of the strains, and few attempts have been made to verify strains available. In Utah only DPG maintains any identified strains.

Although numerous variant strains occur in nature, workers have agreed to accept types A and B (or their counterpart names in references to this disease). While these concepts are not necessarily germane to current studies, it is necessary to recognize the problems that numerous strains, which are always present in nature, pose in everyday studies.

Recent contributions made by personnel at DPG include evidence that the pathogen exists in virtually all areas where specimens are collected regularly, that nonaquatic hosts and their vectors seem to harbor the more virulent Type A (*F. t. tularensis*), and that rodent hosts seem involved superficially. The role of jackrabbits in maintenance and transfer of tularemia is poorly understood. Serum specimens with high titers are most frequently found among carnivores, which apparently do not develop overt symptoms but maintain antibodies to *F. tularensis* for a long time, and livestock that are exposed to vectors. As with jackrabbits, the part that carnivores and livestock have in epizootiology of tularemia is unclear. Although some birds are susceptible, the pathogen passes from birds with difficulty. They probably play no role in epizootiology in the Great Basin. Levels of serum agglutinins among various species of mammals correspond well both geographically and in time. As the antibody levels rise slightly in rodents and lagomorphs, a concomitant increase is found in serum samples of carnivores and livestock. Tests by the former Plague Laboratory in San Francisco and at DPG indicate that fleas are probably not vectors.

To improve our knowledge of epizootiology of the disease, one needs a clearer understanding of the role of jackrabbits in transmitting tularemia and whether tremendous fluctuations in population density affect frequency of transmission. Also needed is a knowledge of strain differences and whether virulence changes in a given area over a period of time. Finally, a determination should be made of the regression and subsequent occurrence of tularemia during apparent interepizootic times with regard to geographic sites, ecologic niches, and primary hosts and vectors. Because of the variety of conditions under which the disease occurs, Utah appears to be a prime area for study.

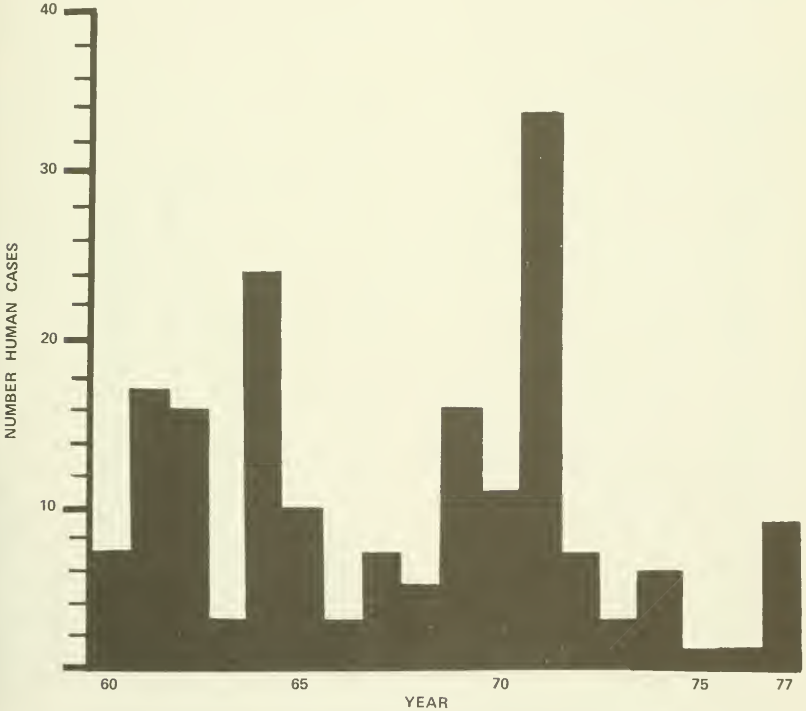

Fig. 2. Annual occurrence of tularemia in humans in Utah, 1960–1977.

## Acknowledgments

Appreciation is expressed to the following, who offered advice and consultation during the preparation of the manuscript: J. F. Bell, G. L. Choules, G. T. Crane, T. W. Edwards, T. Fukushima, A. T. Hereim, C. E. Hopla, W. L. Jellison, W. L. Krinsky, P. S. Nicholes, C. F. A. Pinkham, T. J. Quan, H. B. Rees, Jr., M. A. Rothenberg, L. L. Salomon, J. C. Spendlove, V. J. Tipton, and C. M. Wheeler. Dr. Pinkham suggested the study of human tularemia by statistical analysis and used a program which he prepared. Initial stages of this account arose from a research grant proposal prepared by Dr. Tipton.

Research on which this report is based was supported by Department of Army Project IT0061101A91A (In-House Laboratory Independent Research).

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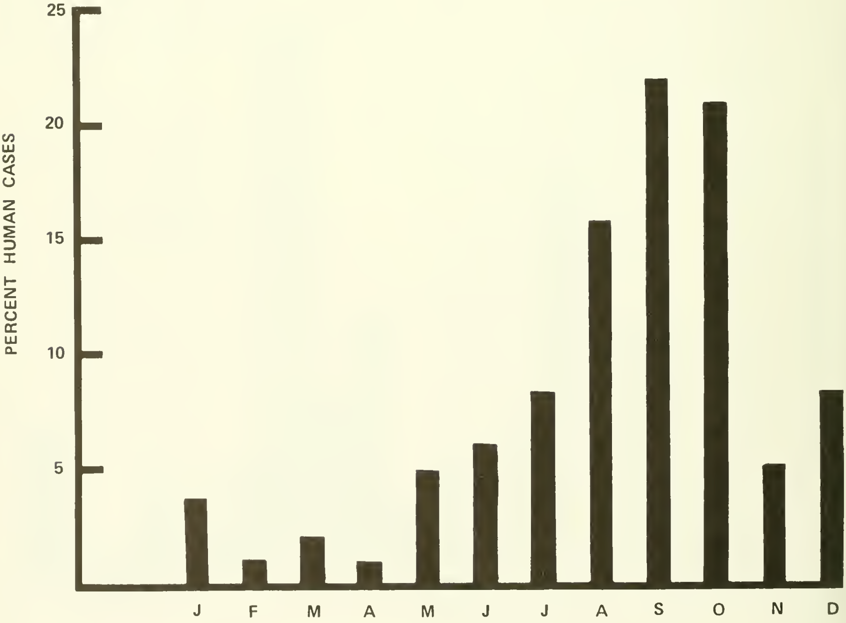

Fig. 3. Monthly occurrence of tularemia in Utah, 1961–1977.

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# CHEMICAL COMPOSITION OF SOME IMPORTANT PLANTS OF SOUTHEASTERN UTAH SUMMER RANGES RELATED TO MULE DEER REPRODUCTION[1]

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Abstract.— Chemical composition of some major forage plants of mountain summer ranges of southeastern Utah is reported. Grasses are shown to contain significantly less nitrogen, phosphorus, potassium, calcium, and magnesium than either forbs or shrubs. Forbs and shrubs are demonstrated to differ significantly only in potassium content; forbs tested contained more potassium than shrubs. The chemical composition of the forage plants is discussed in relation to mule deer reproductive rates. It is concluded that protein and mineral content of the forage of the two ranges considered (the LaSal and Henry mountains) is less likely to affect reproductive rates than is the relative digestibility of grasses, forbs, and shrubs.

The quality of summer forage has been demonstrated to have an effect on body condition, general health, and reproductive capacity of deer (Longhurst et al. 1952, Swank 1956, 1958, Julander et al. 1961, Verme 1962, 1963, Yoakum 1965, Nordan et al. 1968, Snider and Asplund 1974). If the comparative performance of deer on different ranges is to be understood, the nutritional composition of forages consumed on both summer and winter ranges must be known. It is the objective of this paper to provide information on the chemical composition of some important forage plants of the LaSal and Henry mountains of southeastern Utah. Previous work has shown that mule deer (*Odocoileus hemionus*) herds on those mountain ranges differ markedly in respect to reproductive rate (Pederson and Harper 1978). Pederson and Harper (1978) suggested that differences in quality of forage on summer ranges of the two mountain ranges might be responsible for the observed difference in fawn production.

Dietary requirements for whitetailed deer (*Odocoileus virginianus*) have been reported by French et al. (1956), McEwen et al. (1957), Murphy and Coates (1966), Verme (1963, 1965, 1967, 1969), Ullrey et al. (1967, 1971), and Thompson et al. (1973). Although there is little habitat overlap between whitetails and mule deer, it seems likely that nutritional data compiled for whitetails will have some relevance for mule deer nutrition and management. Studies on mule deer food habits and nutrition have been made by Hagen (1939), Bissell et al. (1955), Swank (1956), Urness et al. (1971), McCullock and Urness (1973), Robinette et al. (1973), Urness et al. (1975), and Pack (1976).

Recent investigations have demonstrated that Rocky Mountain mule deer herds resident on the LaSal Mountains produce about 40 percent more fawns per 100 does than do Henry Mountain herds (Pederson and Harper 1978). In an attempt to identify factors responsible for observed reproductive differences, range condition, diseases, and parasites, as well as late winter body conditions of the deer, were evaluated over an eight-year period on the two mountains. Results demonstrated that deer averaged larger per sex and age class on the LaSals than on the Henry Mountains, but neither diseases nor parasites differed significantly between herds. Likewise, deer taken from the two herds could not be shown to differ significantly in respect to body condition in late winter. Winter ranges used by the two herds were similar in respect to both composition and production. In contrast, annual summer forage produc-

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tion on the LaSals averaged almost 65 percent greater than on the Henries (Pederson and Harper 1978). Composition of the forage crop on summer ranges also differed sharply between mountains, with LaSal ranges being dominated by good-quality forbs while Henry Mountain summer ranges were heavily dominated by shrubs and grasses (Pederson and Harper 1978).

In this report, the hypothesis that forage conditions on the summer range are responsible for the greater productivity of the LaSal Mountain deer herd will be investigated. Emphasis is concentrated on nutritional characteristics of major forage species of summer ranges utilized by the two herds.

We greatly acknowledge the help and support given by the following Utah Wildlife Resources personnel: H. D. Stapley, N. V. Hancock, K. L. Nelson, A. Fleck, L. Hall, and N. K. Larsen. Thanks is extended to A. C. Rencher for his help with the statistical analysis of our data and to G. Cronin for her critical review of this manuscript.

## Study Areas

The study areas are in southeastern Utah. The LaSal Mountains are east of Moab in Grand and San Juan counties. The Henry Mountains lie southwest of Hanksville in Wayne and Garfield counties. The two areas are about 117 km apart. Both are laccolithic mountains of similar geologic age (Butler 1920, Hunt et al. 1953). Precipitation averages somewhat higher (about 10 percent) on the LaSals than the Henries for comparable vegetation zones (Pederson 1970).

The LaSal herd unit encompasses approximately 221,374 ha. The highest point on the LaSals is Mount Peale at 3,876 m elevation. The Henry Mountain area includes approximately 72,886 ha; the highest point on the range is Mount Ellen at 3,500 m.

## Methods and Procedures

During late July 1976, a representative range site in the aspen zone of each mountain site was visited. The study site on the LaSals was at Warner Lake; the Henry Mountain site was at Nasty Flats. At each site, an area about one hectare in size was selected in aspen forest. A composite sample of the surface 1.5 dm of soil and the five most common grass, forb, and shrub forage species were collected for subsequent analysis. All aboveground parts of grasses and forbs and current growth (leaves and twigs) of shrub species were taken. Only grasses and forbs in flowering condition were collected; most shrub species were not in flower. Individual plants of each species were collected until a composite sample of over 75 g fresh weight was acquired. Samples were lightly packed in paper bags and oven dried at 80 C within 48 hours of harvest.

Soil samples were air dried, passed through a 2 mm sieve, and delivered to a commercial, analytical laboratory. Soil pH was determined on a 1:1 soil-to-water mixture with a glass electrode meter. Texture was determined using the hydrometer method, and exchangeable cations were extracted with neutral ammonium acetate and determined by atomic absorption procedures. Nitrogen was measured using micro-Kjeldahl apparatus. Soil organic matter was determined by loss-on-ignition.

Dried plant samples were ground through a 40-mesh sieve in a standard mill. Samples were stored in glass containers until the analyses were completed. Estimates of crude protein were based on total nitrogen as determined by micro-Kjeldahl procedures. All other elements were determined from ash, using standard atomic absorption and colorimetric techniques (American Society of Agronomy 1965).

Differences in chemical composition between species belonging to different life form groups (i.e., grasses, forbs, and shrubs) on the same mountain range and between life forms on different mountain ranges were determined using analysis of variance and Duncan multiple range test. Statistical procedures follow Snedecor and Cochran (1967).

## Results

Soils of the two study sites are both of loamy texture (Table 1). Soils at the LaSal study area were slightly more acidic than those at the Henry site. Soil organic matter and nitrogen content were somewhat higher at the LaSal Mountain study area; both variables probably reflect a somewhat better moisture balance at the LaSal site. Soils from the Henry Mountain site have considerably higher phosphorus content and generally higher exchangeable cation levels than the LaSal soils (Table 1).

Chemical composition of the current year, aboveground growth of major species, and current-year twig growth of important browse species of the summer ranges of the LaSal and Henry mountains are reported in Table 2. Average values for grasses differ significantly between mountain ranges. Species from the LaSals contain more nitrogen, potassium, calcium, and magnesium. Phosphorous content of grasses did not differ significantly between mountain ranges. Shrubs of the two mountain ranges differed significantly for nitrogen only, with LaSal shrubs averaging 40 percent more nitrogen than the Henries. Elemental content of plants was strongly correlated with soil content of the same element for nitrogen and phosphorous only. Other elements showed little correlation between amounts in plants and associated soils.

The elemental content of grasses (all species polled) was significantly lower than for either forbs or shrubs for all elements tested. Few significant differences in chemical composition could be demonstrated between forbs and shrubs. Only the potassium content of forbs could be shown to differ significantly from that of shrubs—potassium averaged 138 percent higher in forbs (Table 2).

The average contribution of grasses, forbs, and shrubs to the forage crop of summer ranges of the LaSals and Henries is shown in Table 3. Furthermore, several analyses of the relative preference of mule deer for grasses, forbs, and shrubs during the summer season have been reported (Table 4). Because estimates of chemical (Table 2) and botanical (Table 3) composition of the summer range forage crop of the LaSal and Henry mountains are available, it is possible to combine those data with feeding preference information for mule deer (Table 4) and obtain estimates of the chemical composition of the summer diet of deer on the two ranges.

Assuming deer select grasses, forbs, and shrubs in the proportions reported by any author in Table 4, regardless of the abundance in the vegetation of plants in each life form category, the composition of the diet can be estimated for any element in either of the study areas. For example, to estimate the amount of phosphorus in diets of LaSal mule deer, assuming a feeding preference such as that reported by Smith (1952) in Table 4, sum the products of (1) average percent phosphorus in LaSal grasses times the proportion of grasses in mule deer diets reported by Smith, (2) average percent phorphorus in LaSal forbs times the proportion of forbs in the diet, and (3) the average percent phosphorus in LaSal shrubs times the proportion of shrubs in the diet. For this example, we estimate that mule deer diets on the LaSals should contain .18 percent phosphorus.

The chemical composition of four alternative diets has been estimated in Table 5. Three diets are based on feeding preferences reported by Smith (1952), Morris and Schwartz (1957), and Trout and Thiessen (1968). The fourth diet is based on the assumption that the deer select grasses, forbs,

TABLE 1. Chemical and physical characteristics of soils on the LaSal and Henry mountains study areas.

| | | | | | ANALYSIS | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Mountain range | pH | Sand % | Silt % | Clay % | Organic matter % | Nitrogen % | Phosphorus ppm | Potassium ppm | Calcium ppm | Magnesium ppm |
| LaSal Mountains Warner Lake | 6.3 | 48 | 46 | 6 | 8.11 | 0.47 | 14.0 | 417.6 | 2090.4 | 105.6 |
| Henry Mountains Nasty Flats | 6.7 | 50 | 38 | 12 | 6.04 | 0.35 | 42.4 | 420.0 | 2822.4 | 166.4 |

and shrubs in exact proportion to their abundance in the vegetation. The results show chemical composition of diets differs relatively little regardless of the assumption used (Table 5). Furthermore, estimated chemical composition of diets does not differ radically between mountain ranges. Even the lowest estimates for each dietary constituent studied appear to be within safe limits for good animal health (Dasmann 1971, Morrison 1961). The calcium/phosphorous ratio also seems to be within normal limits (Table 5).

## DISCUSSION

The results indicate that differences in plant chemistry between the two mountain ranges for the elements considered in this paper are probably not responsible for the observed reproductive differences between mule deer herds resident on the two mountain ranges. However, it cannot be concluded that summer range forage is not responsible for the observed differences in deer reproduction. The digestible energy content is unknown for the species considered in this re-

TABLE 2. Chemical composition of current year, aboveground growth of some major forage species of the summer ranges of the LaSal (L) and Henry (H) mountains of southeastern Utah. Specimens for analysis were collected on 26 and 27 July 1976. Composition values have been averaged by plant life form group and mountain range.

| SPECIES | NITROGEN | | PHOSPHORUS | | POTASSIUM | | CALCIUM | | MAGNESIUM | |
|---|---|---|---|---|---|---|---|---|---|---|
| | L | H | L | H | L Percent | H | L | H | L | H |
| GRASSES | | | | | | | | | | |
| *Agropyron trachycaulum* | 1.51 | 0.91 | 0.12 | 0.12 | 1.88 | 0.89 | 0.26 | 0.27 | 0.07 | 0.08 |
| *Bromus carinatus* | 1.79 | – | 0.17 | – | 2.60 | – | 0.44 | – | 0.12 | – |
| *Carex geyeri* | 1.16 | – | 0.12 | – | 1.81 | – | 0.34 | – | 0.13 | – |
| *Elymus glaucus* | 1.82 | – | 0.13 | – | 2.61 | – | 0.35 | – | 0.09 | – |
| *Festuca ovina* | – | 1.30 | – | 0.11 | – | 1.06 | – | 0.26 | – | 0.07 |
| *Festuca thurberi* | – | 0.99 | – | 0.10 | – | 1.75 | – | 0.22 | – | 0.07 |
| *Sitanion hystrix* | – | 1.15 | – | 0.11 | – | 1.64 | – | 0.17 | – | 0.06 |
| *Stipa columbiana* | 1.19 | 1.11 | 0.12 | 0.13 | 1.82 | 1.55 | 0.33 | 0.33 | 0.08 | 0.08 |
| Average by mountain range | 1.50$^{a}$ | 1.09$^{b}$ | 0.13$^{a}$ | 0.11$^{a}$ | 2.14$^{a}$ | 1.38$^{b}$ | 0.35$^{a}$ | 0.25$^{b}$ | 0.10$^{a}$ | 0.07$^{b}$ |
| Pooled average | 1.305$^{c}$ | | 0.123$^{c}$ | | 1.762$^{c}$ | | 0.300$^{c}$ | | 0.085$^{c}$ | |
| FORBS | | | | | | | | | | |
| *Chenopodium fremontii* | – | 3.14 | – | 0.25 | – | 7.90 | – | 1.18 | – | 0.76 |
| *Erigeron speciosus* | 1.77 | – | 0.18 | – | 3.35 | – | 1.01 | – | 0.15 | – |
| *Helianthella quinquenervis* | 1.62 | – | 0.23 | – | 4.53 | – | 1.65 | – | 0.28 | – |
| *Hymenoxys richardsonii* | – | 1.54 | – | 0.20 | – | 3.05 | – | 1.29 | – | 0.26 |
| *Ligusticum porteri* | 1.55 | – | 0.19 | – | 4.74 | – | 1.34 | – | 0.25 | – |
| *Lupinus parviflorus* | 2.49 | – | 0.15 | – | 2.29 | – | 1.44 | – | 0.34 | – |
| *Oxytropis sericeus* | – | 1.92 | – | 0.18 | – | 1.91 | – | 0.98 | – | 0.16 |
| *Penstemon watsonii* | – | 1.12 | – | 0.15 | – | 1.88 | – | 1.16 | – | 0.26 |
| *Senecio ambrosioides* | – | 1.62 | – | 0.19 | – | 3.24 | – | 1.01 | – | 0.23 |
| *Thalictrum fendleri* | 1.44 | – | 0.19 | – | 2.19 | – | 0.87 | – | 0.12 | – |
| Average by mountain range | 1.77$^{a}$ | 1.87$^{a}$ | 0.18$^{a}$ | 0.19$^{a}$ | 3.42$^{a}$ | 3.59$^{a}$ | 1.26$^{a}$ | 1.12$^{a}$ | 0.23$^{a}$ | 0.33$^{a}$ |
| Pooled average | 1.820$^{d}$ | | 0.192$^{d}$ | | 3.509$^{d}$ | | 1.195$^{d}$ | | 0.281$^{d}$ | |
| SHRUBS | | | | | | | | | | |
| *Artemisia tridentata vaseyana* | – | 1.92 | – | 0.20 | – | 2.09 | – | 0.49 | – | 0.15 |
| *Populus tremuloides* | 1.96 | 1.51 | 0.13 | 0.15 | 1.06 | 1.38 | 1.20 | 0.60 | 0.20 | 0.17 |
| *Prunus virginiana* | 2.57 | – | 0.30 | – | 1.55 | – | 1.71 | – | 0.33 | – |
| *Ribes cereum* | – | 1.19 | – | 0.20 | – | 1.02 | – | 0.94 | – | 0.26 |
| *Rosa woodsii* | 1.84 | 1.86 | 0.19 | 0.22 | 1.09 | 1.27 | 1.03 | 1.59 | 0.33 | 0.38 |
| *Salix lasiandra* | 2.59 | – | 0.16 | – | 1.29 | – | 1.33 | – | 0.26 | – |
| *Symphoricarpos oreophilus* | 1.86 | 1.23 | 0.17 | 0.18 | 1.90 | 2.08 | 1.10 | 0.63 | 0.29 | 0.23 |
| Average by mountain range | 2.16$^{a}$ | 1.54$^{b}$ | 0.19$^{a}$ | 0.19$^{a}$ | 1.38$^{a}$ | 1.57$^{a}$ | 1.27$^{a}$ | 0.85$^{a}$ | 0.28$^{a}$ | 0.24$^{a}$ |
| Pooled average | 1.853$^{d}$ | | 0.191$^{d}$ | | 1.474$^{d}$ | | 1.064$^{d}$ | | 0.262$^{d}$ | |

Superscripts a and b are used to indicate significance of difference ($P<0.05$ or better) of averages for a specific plant life form and nutrient element between mountain ranges. Pooled averages for a specific lifeform and element on both mountain ranges were tested for statistically significant differences from pooled averages of the same element in other life form groups on the same mountain ranges. Pooled averages that differ significantly ($P<0.05$ or better) have different superscripts (i.e., c and d); averages that do not differ significantly are followed by the same letter.

port, but there is evidence that deer are unable to digest shrub tissue well enough to supply adequate energy for even maintenance requirements (Nordan et al. 1968, Walmo et al. 1977). Much data exist to show that forbs are generally more digestible than is shrub tissue (Nordan et al. 1968, Torgerson and Pfander 1971, Short 1971, Urness 1973, Snider and Asplund 1974, Walmo et al. 1977). The data also suggest that grasses are more digestible than shrubs. If deer diets on the two mountains do diverge widely in respect to the mix of forbs, grasses, and shrubs, summer range forage may exert a significant influence on deer reproduction through the energy component of the diets.

Table 3. Average relative contribution by weight of grasses, forbs, and shrubs to the forage crop of summer ranges on the LaSal and Henry mountains. Data from Pederson and Harper (1978, Table 4).

| Plant group | Mountain Range | |
|---|---|---|
| | LaSals | Henries |
| | Percent | |
| Grasses | 21 | 13 |
| Forbs | 52 | 12 |
| Shrubs | 27 | 75 |

As noted in Table 3, the LaSal and Henry Mountains do differ greatly in composition of the forage crop of their summer ranges. Pederson (1970) has shown that the LaSals not only produce more forb biomass than the Henries, but that they also have about twice as many forb species for deer to select from as do the Henries (i.e., 90 forbs species sampled on the LaSals compared to 45 sampled on the Henries). Given the great difference between summer ranges on the two mountains, it seems likely that Henry Mountain deer consume more shrub and less forb tissue in summer diets than do animals on the LaSals.

Does that feed heavily on shrubs may have difficulty meeting the energy demands of daily maintenance, lactation, and weight gains required to compensate for weight lost on winter ranges. Cook's (1972) data suggest that stress will be most severe in late summer. Does that do become stressed by late season energy deficits could respond to the stress in at least three ways: (1) continue to lactate heavily at the expense of personal body condition, (2) lactate poorly and reduce body condition of the fawn and self, or (3) abandon the fawn and devote more energy to personal well-being. Option (1) would keep

Table 4. Relative dietary intake (percent by volume) of plants of different life form groups by mule deer on summer ranges.

| Location | Percent intake of | | | Source of data |
|---|---|---|---|---|
| | Grasses | Forbs | Shrubs | |
| Southwestern Idaho | 10 | 9 | 81 | Trout and Thiessen (1968) |
| Western Montana | 1 | 70 | 29 | Morris and Schwartz (1957) |
| Northern Utah | 5 | 68 | 27 | Smith (1952) |

Table 5. Comparative chemical composition of four possible mule deer diets on the LaSal and Henry mountains of southeastern Utah.

| | LaSal Mountains | | Henry Mountains | | |
|---|---|---|---|---|---|
| | Average % in four diets | Range | Average % in four diets | Range | % differences based on averages |
| Protein | 11.9 | 11.6 -12.9 | 10.2 | 9.5 -11.0 | 17 (LaSals higher) |
| Phosphorus | .18 | .17- .18 | .18 | .18- .19 | 5 (Henries higher) |
| Potassium | 2.5 | 1.6 - 2.8 | 2.4 | 1.7 - 3.0 | 5 (LaSals higher) |
| Calcium | 1.2 | 1.1 - 1.3 | .9 | .8 - 1.0 | 29 (LaSals higher) |
| Magnesium | .24 | .22- .26 | .26 | .23- .30 | 9 (Henries higher) |
| Calcium/phosphorus | 6.7 | 6.5 - 7.2 | 5.0 | 4.4 - 5.3 | 34 (LaSals higher) |

fawn survival high, but lower doe survival; option (2) would reduce survival of both does and fawns; and option (3) would drastically reduce fawn survival, but contribute to better doe survival. Low fawn production on the Henries may indicate that does there are exercising option (2) or (3) or both.

The differential fawn production on the LaSal and Henry mountains could be better understood if the composition of summer diet in the two herds was known. With such data, digestibility studies of the major plant components in the diet could be made. Fortunately, recent developments in fecal pellet analysis make it possible to obtain direct information about dietary composition at reasonable costs (Vavra et al. 1978). Plant digestibility can be economically estimated with *in vitro* methods (Urness 1973, Snider and Asplund 1974).

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# EMERGENCE DATA AND ARTIFICIAL REARING MEDIA FOR AN ASPEN BARK BEETLE, *TRYPOPHLOEUS POPULI* (COLEOPTERA: SCOLYTIDAE)

David A. Stewart[1], Gary M. Booth[1], and Jerold L. Petty[1,2]

Abstract.— The aspen bark beetle, *Trypophloeus populi* Hopkins, was studied in nature to determine the number of larvae emerging from galleries. Fifty-five percent of the larvae in aspen galleries in the field developed into adults. An artificial rearing medium for third instar larvae of the beetles was also developed from aspen bark sawdust and nutrient agar. The optimum medium contained a ratio of 1:2 parts of agar to sawdust which gave 70 percent emergence of the beetles and less than 10 percent of adult mortality over the 36 days following emergence.

The bark beetle *Trypophloeus populi* Hopkins has been reported from 13 localities in North America, 6 of which are in northern Utah (Wood, in preparation). Petty (1977) conducted an in-depth study of the bionomics of *T. populi* and compared it to another aspen bark beetle *Procryphalus mucronatus* (LeConte). Later, *T. populi* became the focus of a study on the larvicidal effects of the insecticide dimilin on bark beetles (Stewart, Booth, and Petty, in preparation). Except for two brief taxonomic studies on European *Trypophloeus* (Hagedorn 1904, Palm 1959), nothing else has been published on the bionomics of this genus.

The objectives of this paper are: (1) to report the development of an artificial medium for rearing *T. populi* and (2) to determine the percent emergence of *T. populi* in nature.

## Materials and Methods

The beetle larvae were collected from two sites in Utah county, Utah. The first site was 1.6 km north of Aspen Grove, and the second site was 1.8 km north of Aspen Grove. Collections were made by removing strips of infested *Populus tremuloides* bark with a hand ax. Larvae were then removed in the laboratory from the bark sections by breaking open larval galleries.

Counts of the emergence holes per parental galley system in previously infested *P. tremuloides* trees were conducted at both collecting sites. A transparent 10 cm square grid was randomly placed on the trees to make the counts. Larvae in parental galleries were counted as removed from 10 cm square areas of infested bark.

Four artificial media were prepared from the sawdust of aspen bark cut by a radial-arm saw, which was then mixed with varying amounts of nutrient agar and autoclaved at 6.8 kg pressure and 110 C for 15 minutes to suppress microorganism activity (Bedard 1966). Petri dishes containing 30 grams of the medium were stored and used at 22 C. The larvae were transferred into the medium using strict sterile techniques.

## Results and Discussion

The average number of larvae found per gallery in nature during this study was 14.75 (Table 1). Petty (1977) reported 14 eggs per primary egg chamber for *T. populi* and often found two or three other secondary areas where eggs were deposited in smaller numbers. However, there was no estimate of the total number of eggs per gallery.

Each newly emerging adult *T. populi* exits from the tree by boring out, leaving a small hole in the bark surface to indicate its departure (Petty 1977). By counting these holes, an estimate of the number of adult beetles that developed from the larvae was found to be 8.16 per galley (Table 2). Dividing the number of exit holes made by emerging adults by the estimated number of larvae indicates that 55 percent of the larvae developed into adults that emerged from the tree.

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TABLE 1. Average number of *Trypophloeus populi* larvae per parental gallery in random 10 × 10 cm squares.

| Number of galleries per sample | Total larvae found | Larvae per gallery |
|---|---|---|
| 7 | 119 | 17.0 |
| 7 | 106 | 15.14 |
| 7 | 121 | 17.29 |
| 6 | 156 | 26.00 |
| 6 | 68 | 11.33 |
| 6 | 90 | 15.00 |
| 6 | 111 | 18.50 |
| 5 | 60 | 12.00 |
| 5 | 69 | 13.80 |
| 5 | 50 | 10.00 |
| 4 | 48 | 12.00 |
| 4 | 39 | 9.75 |
| 4 | 67 | 16.75 |
| 4 | 40 | 10.00 |
| 3 | 46 | 15.33 |
| 3 | 39 | 13.00 |
| 3 | 41 | 13.67 |
| 2 | 32 | 16.00 |
| 2 | 26 | 13.00 |
| 2 | 6 | 3.00 |
| 2 | 35 | 17.50 |
| 2 | 48 | 24.00 |
| 1 | 7 | 7.00 |
| 1 | 20 | 20.00 |
| 1 | 13 | 13.00 |
| 1 | 19 | 19.00 |
| 1 | 26 | 26.00 |
| 1 | 4 | 4.00 |
| 1 | 13 | 13.00 |
| 1 | 18 | 18.00 |
| 1 | 21 | 21.00 |
| 104 | 1558 | 14.75 ± 6.10 |

From 1 to 20 larvae were placed on the artificial media. Development data indicate no significant difference due to number of larvae at the .05 level using the standard t test. Pure nutrient agar and pure sawdust were compared to the results obtained from the media. Emergence of the adults occurred from 21 to 28 days after being placed on the media, and pupation occurred at 16 to 21 days. All larvae placed on the media were of the third or final instar as determined by head capsule size (Petty 1977). Larvae of the first two instars were also successfully reared but records were not kept on them.

Emergence varied from 1.67 percent of the larvae (on pure nutrient agar) to 70 percent of the larvae (two parts bark to one part agar, Table 3). Many of the larvae were able

TABLE 2. Number of *Trypophloeus populi* emergence holes per parental gallery in random 10 × 10 cm squares.

| Number of galleries per sample | Number of emergence holes | Emergence per gallery |
|---|---|---|
| 12 | 82 | 6.83 |
| 8 | 91 | 11.38 |
| 6 | 39 | 6.50 |
| 13 | 100 | 7.69 |
| 6 | 56 | 9.33 |
| 7 | 78 | 11.14 |
| 8 | 91 | 11.38 |
| 9 | 83 | 9.22 |
| 8 | 79 | 9.88 |
| 6 | 68 | 11.33 |
| 11 | 85 | 7.73 |
| 7 | 44 | 6.29 |
| 8 | 72 | 9.00 |
| 7 | 66 | 9.43 |
| 6 | 47 | 7.83 |
| 5 | 28 | 5.60 |
| 5 | 21 | 4.20 |
| 4 | 12 | 3.00 |
| 3 | 22 | 7.33 |
| 139 | 1164 | 8.16 ± 2.42 |

TABLE 3. Results of an artificial rearing medium for *Trypophloeus populi*.

| Medium, parts agar:bark | Number of larvae | Number emerged | Percent emerged | Percent Dead 36 days after emergence |
|---|---|---|---|---|
| 1:0 | 60 | 1 | 2 | 100 |
| 2:1 | 80 | 15 | 18 | 58 |
| 1:1 | 233 | 76 | 31 | 29 |
| 1:2 | 95 | 67 | 70 | 7 |
| 1:3 | 50 | 20 | 40 | 7 |
| 0:1 | 77 | 48 | 65 | 98 |

to develop into adults but were unable to feed on the medium and subsequently died shortly after (Fig. 1). It is interesting that the pure sawdust medium caused 98 percent mortality of the larvae after 36 days. This high mortality could have been possibly caused by changes in moisture content, but no attempt was made to investigate this possibility. Adults feeding on two parts bark to one part agar and three parts bark to one part agar lived on the medium up to 120 days. They constructed galleries but oviposition did not occur.

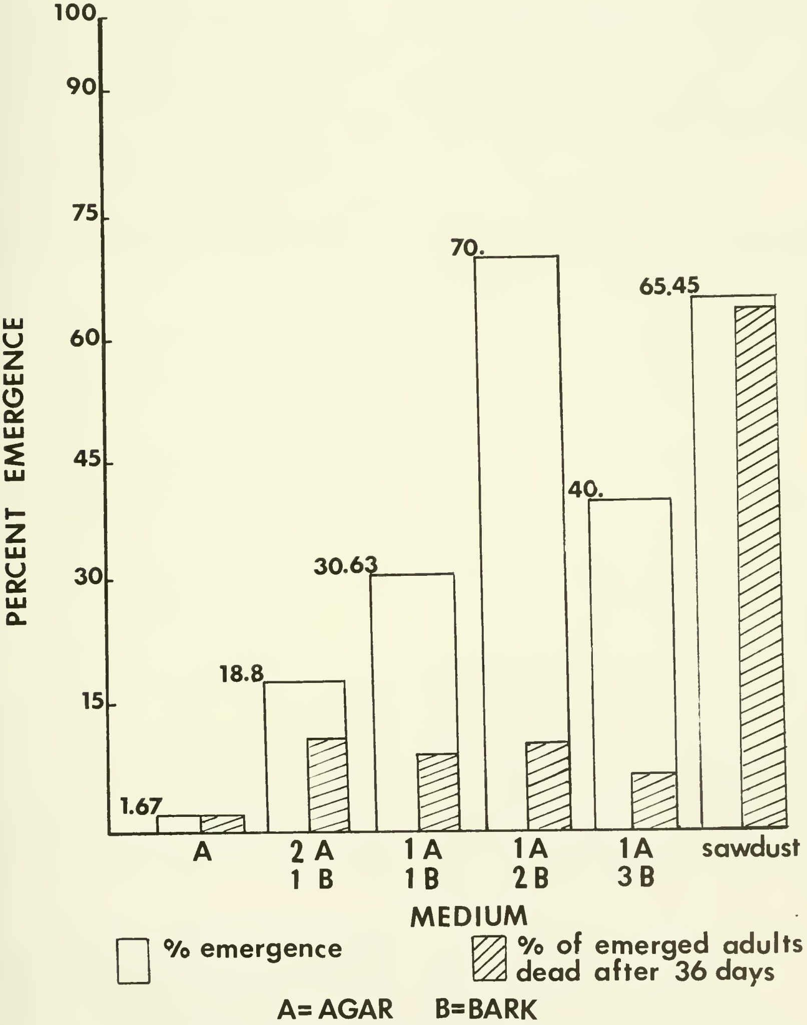

Fig. 1. Percent emergence of *Trypophloeus populi* in artificial media and percent of emerged adults dead after 36 days.

## SUMMARY

In nature it was estimated that 55 percent of the larvae produced in a gallery will develop into adults and emerge.

The bark beetle *Trypophloeus populi* was reared from the third instar larva to the adult stage on a medium of nutrient agar and aspen bark sawdust. The optimum concentration of bark to agar was two parts bark to one part agar, with 70 percent of the larvae developing into adults. Adults fed on the medium and excavated galleries, but mating and oviposition were not observed.

## ACKNOWLEDGMENTS

We wish to acknowledge the expertise and assistance of Dr. Stephen L. Wood, who offered counsel and encouragement throughout the project.

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# NEW SYNONYMY AND NEW SPECIES OF AMERICAN BARK BEETLES (COLEOPTERA: SCOLYTIDAE), PART VIII[1]

Stephen L. Wood[2]

Abstract.— New synonymy of American Scolytidae is proposed as follows: *Acacacis*, Lea (=*Neodiamerus* Schedl), *Gnatholeptus panamensis* Blackman (=*Pityophthorus epistomalis* Schedl), *Gnatholeptus shannoni* (Blackman) (=*Gnatholeptus mandibularis* Blackman, *Pityophthorus gentilis* Schedl), *Gymnochilus reitteri* Eichhoff (=*Problechilus striatus* Eggers, *Problechilus bicolor* Eggers), *Hylastes scabripennis* (Zimmermann) (=*Hylastes salebrosus* Eichhoff), *Hylurgopinus opaculus* (LeConte) (=*Hylastes rufipes* Eichhoff), *Ips perturbatus* (Eichhoff) (=*Tomicus interpunctus* Eichhoff), *Monarthrum dimidiatum* (Ferrari) (=*Pterocyclon moritzi* Eichhoff), *Pityophthorus subcribratus* Schedl (=*Pityophthorus zeteki* Blackman), *Scolytodes trispinosus* Eggers (=*Scolytodes elongatus* Schedl), *Xyleborus costaricensis* Blandford (=*Xyleborus nevermanni* Schedl), *Xyleborus improvidus* Schedl (=*Xyleborus aclinus* Wood), *Xyleborus spinulosus* Blandford (=*Xyleborus fusciseriatus* Eggers, *Xyleborus artespinulosus* Schedl). The genus *Carphodicticus* Wood is removed from synonymy with *Dendrodicticus* Schedl. *Scolytodes striatulus*, new name, is proposed as a replacement for *Hylocurosoma striatum* Eggers. Notes on the status of *Xyleborus perforans* (Walker) are presented. The following species are named as new to science: *Cnemonyx furvescens* (Colombia), *C. squamifer* (Guatemala), *C. protivorus* and *C. vismiacolens* (Venezuela), *Corthylus nanus* (Costa Rica), *Dendrocranulus auctus*, *D. limbellus*, *D. limitaris*, *D. modus*, and *D. pinguis* (Venezuela), *Hylocurus clarki* (Guatemala), and *H. longipennis* (Mexico).

On the following pages several newly discovered cases of synonymy, some additional notes, and 12 species new to science are presented for American Scolytidae. The species new to science represent the genera *Cnemonyx* (4), *Corthylus* (1), *Dendrocranulus* (5), and *Hylocurus* (2) and were taken in Mexico (1), Guatemala (2), Costa Rica (1), Colombia (1), and Venezuela (7).

## New Synonymy and Notes

### *Acacicis* Lea

*Acacicis* Lea, 1910, Proc. Roy. Soc. Victoria 22:149 (Type-species: *Acacicis abundans* Lea, monobasic)

*Neodiamerus* Schedl, 1971, Ent. Scand. (Suppl.) 1:282 (Type-species: *Neodiamerus granulicollis* Schedl, original designation). *New synonymy*

The unique male holotype of *Neodiamerus granulicollis* Schedl and 102 other specimens of this species were compared to eight species of *Acacicis*, including two paratypes and more than 100 other species of *A. abundans* Lea. In the absence of anatomical or biological characters that might distinguish them, it is necessary to place *Neodiamerus* in synonymy and to transfer *granulicollis* to *Acacicis*.

### *Dendrodicticus* Schedl

*Dendrodicticus* Schedl, 1958, Acta Zool. Lilloana 16:37 (Type-species: *Dendrodicticus argentiniae* Schedl, original designation)

Schedl (1975, Ent. Blätt. 71:42) placed *Carphodicticus* Wood (1971, Brigham Young Univ. Sci. Bull., Biol. Ser. 15(3):19) in synonymy under his *Dendrodicticus*. My examination of the type of *D. argentiniae* Schedl suggests that a reevaluation of this action is necessary. Schedl's type appears to be a female that superficially resembles *C. cristatus* Wood. However, the antennal club is more slender, symmetrical, and the sutures are entirely transverse (broader, distinctly asymmetrical, with sutures slightly oblique in *C. cristatus*), the procoxae are more widely separated, the tibiae are longer, more slender,

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and apparently have a different arrangement of socketed denticles, the pronotum is less elongate and feebly constricted, the basal margins of the elytra are strongly elevated into an irregular (subcrenulate) costa, the declivital impression is deeper and the lateral convexities are higher and extend the full length of the declivity, and the elytral vestiture is represented by closely set rows of fine strial and coarse interstrial setae from the base to the apex except on declivital interstriae 2. While the two species are of somewhat similar size and appearance, the antennal, tibial, pronotal, and elevated basal margins of the elytra in *Dendrodicticus* suggests that Schedl's action was premature. Until other species are found that reduce the character gap between these two taxa, they should be considered as distinct genera. The type of *D. argenteniae* is in rather poor condition and several important characters are hidden; however, until more material is available for study I tentatively place it in the tribe Carphodicticini.

### *Gnatholeptus panamensis Blackman*

*Gnatholeptus panamensis* Blackman, 1943, J. Washington Acad. Sci. 33:35 (Holotype, female; Barro Colorado Island, Canal Zone, Panama; U.S. Nat. Mus.)

*Pityophthorus epistomalis* Schedl, 1961, Pan Pacific Ent. 37:224 (Holotype, female; Barro Colorado Island, Canal Zone, Panama; Cornell Univ.) *New synonymy*

The female holotypes of *Gnatholeptus panamensis* Blackman and *Pityophthorus epistomalis* Schedl were compared to my series of 29 specimens from Costa Rica and Panama. Because only one distinctive species is represented by this material, Schedl's name must be placed in synonymy as indicated above.

### *Gnatholeptus shannoni* (Blackman)

*Pityophthorus shannoni* Blackman, 1942, Proc. U.S. Nat. Mus. 92:224 (Holotype, female; Cano Saddle at Gatun Lake, Canal Zone, Panama; U.S. Nat. Mus.)

*Gnatholeptus mandibularis* Blackman, 1943, J. Washington Acad. Sci. 33:34 (Holotype, female; Barro Colorado Island, Canal Zone, Panama; U.S. Nat. Mus.). *New synonymy*

*Pityophthorus gentilis* Schedl, 1961, Pan Pacific Ent. 37:225 (Holotype, male; Barro Colorado Island, Gatun Lake, Canal Zone, Panama; Cornell Univ.). *New synonymy*

The holotypes of *Pityophthorus shannoni* Blackman, *P. gentilis* Schedl, and *Gnatholeptus mandibularis* Blackman were compared directly to more than 60 of my specimens from the Canal Zone, Panama. Only one distinctive species is represented in this material.

### *Hylastes scabripennis* (Zimmermann), n. status

*Hylurgus scabripennis* Zimmermann, 1868, Trans. Amer. Ent. Soc. 2:149 (Syntypes; Atlantic States; Mus. Comp. Zool.)

*Hylastes salebrosus* Eichhoff, 1869, Berliner Ent. Zeitschr. 12:146 (Syntypes; Carolina; one in U.S. Nat. Mus.); Blandford, 1898, Ent. News 9:5. *Synonymy*

Although the synonymy of *Hylurgus scabripennis* Zimmermann and *Hylastes salebrosus* Eichhoff was known to Eichhoff (1896, Proc. U.S. Nat. Mus. 18:606) and subsequent workers, it was assumed that Eichhoff's name had priority. Consequently, the name *salebrosus* has been used consistently in American literature during this century. All American workers overlooked Blandford's (1898, Ent. News 9:5) article in which the priority of *scabripennis* (December 1868) is clearly established over *salebrosus* (March 1869). In view of this priority and the time-consuming, difficult process of overriding it, the name *scabripennis* is being used to designate this species.

### *Hylurgopinus opaculus* (LeConte), n. status

*Hylesinus opaculus* LeConte, 1868, Trans. Amer. Ent. Soc. 2:170 (Two syntypes; Pennsylvania; Mus. Comp. Zool.).

*Hylastes rufipes* Eichhoff, 1869, Berliner Ent. Zeitschr. 12:147 (Syntypes; Carolina; one syntypes in U.S. Nat. Mus.); Eichhoff, 1896, Proc. U.S. Nat. Mus. 18:605. *Synonymy*

The synonymy of this species was discussed by Eichhoff (1896, cited above) and has been confirmed by me through the examination of all known syntypes. The assumption was made by Eichhoff and subsequent authors that his name had priority; however, Blandford (1898, Ent. New 9:5) pointed out that *opaculus* was validated in December 1868 and *rufipes* in March 1869. In view of the priority of *opaculus* and the extreme difficulty of overriding priority when the need for correction has been published, as in this case, the name *opaculus* is being restored and used for this species, which has been known as *Hylurgopinus rufipes* during most of this century.

### *Gymnochilus reitteri* Eichhoff

Gymnochilus reitteri Eichhoff, 1878, preprint of Mem. Soc. Roy. Sci. Liége (2)8:169 (Lectotype, male; Mexico; U.S. Nat. Mus., present designation)

*Problechilus striatus* Eggers, 1932, Wiener Ent. Zeit. 49:227 (Holotype, male; Canelas, probably Durango, Mexico; U.S. Nat. Mus.). *New synonymy*

*Problechilus bicolor* Eggers, 1932, Wiener Ent. Zeit. 49:228 (Holotype, male; Nicaragua; U.S. Nat. Mus.). *New synonymy*

Four syntypes of *Gymnochilus reitteri* Eichhoff are in the U.S. National Museum, all mounted on one pin. One of the two males was marked by the word "type" on the mounting card and is here designated as the lectotype as indicated above. It bears Eichhoff's labels "61," "Mex.," and *Problechilus reitteri* Eichh., Type." These syntypes were compared directly to the holotypes of *Problichilus striatus* Eggers and *Problechilus bicolor* Eggers and to 44 other specimens. All represent the same common species.

### *Ips perturbatus* (Eichhoff)

*Tomicus perturbatus* Eichhoff, 1869, Berliner Ent. Zeitschr. 12:274 (Syntypes?, *Amerique boreali*; presumably lost with Hamburg Mus.)

*Tomicus interpunctus* Eichhoff, 1878, preprint of Mem. Soc. Roy. Sci. Liége (2)8:241 (Syntypes?; Sitka, Alaska; presumably lost with Hamburg Mus.). *New synonymy*

Although the type was lost in the destruction of the Hamburg Museum, *Tomicus purturbatus* Eichhoff is recognizable by its size and redescription of the type and from the comparison of the type to specimens of *Tomicus hudsonicus* LeConte by Eichhoff (1878:248–250). The type of *interpunctus* Eichhoff was also lost with the Hamburg Museum, and this name has never been associated with a natural population. The type of *interpunctus* was taken at Sitka, Alaska, where only two species of *Ips* occur, (1) *purturbatus*, and (2) *tridens* (Mannerheim). The original description indicates that the type was 4.0 mm long, it had a transversely arranged pair of tubercles on the frons, and it had the basal area of the discal interstriae impunctate. The size could fit either species, but the other two characters apply only to *purturbatus*. Therefore, *interpunctus* is placed in synonymy under the senior name *perturbatus*. It is conceivable that *pini* (Say) might eventually be found on Sitka Island; however, specimens of *pini* from the northwestern part of its range lack the frontal tubercles.

### *Monarthrum dimidiatum* (Ferrari)

*Corthylus dimidatum* Ferrari, 1867, Die Forst- und Baumzuchtschädlichen Borkenkäfer, p. 57 (Syntypes; Venezuela; Vienna Mus.)

*Pterocyclon moritzi* Schedl, 1939, Rev. de Ent. 10:727 (Holotype, male; locality not given; Schedl Coll.). *New synonymy*

Two male syntypes of *Corthylus dimidiatus* Ferrari, the male holotype of *Pterocyclon moritzi* Schedl, and 33 other specimens from Costa Rica, Colombia, and Venezuela (15 of these were from Colonia Tovar and nearby Rancho Grande in Pittier National Park) were examined. Since both *dimidiatus* and *moritzi* appear to have been named from Moritz material taken at Colonia Tovar, Aragua, Venezuela, it is not surprising that the type specimens are identical to one another and to my series taken in that vicinity. Because only one species is represented, Schedl's name must be placed in synonymy as indicated above.

### *Pityophthorus subcribratus* Schedl

*Pityophthorus subscribratus* Schedl, 1937, Arch. Inst. Biol. Veget. Río de Janeiro 3:168 (Holotype, female; Hamburgfarm on Río Reventazon, Limon, Costa Rica; Schedl Coll.)

*Pityophthorus zeteki* Blackman, 1942, Proc. U.S. Nat. Mus. 92:226 (Holotype, female; Trinidad River, Panama; U.S. Nat. Mus.). *New synonymy*

The female holotypes of *Pityophthorus subcribratus* Schedl and *P. zeteki* Blackman were examined and compared directly to my series of 62 specimens from Costa Rica and Panama. Because only one species is represented by this material, Blackman's name must be placed in synonymy as indicated above.

### *Scolytodes striatulus*, new name

*Hylocurosoma striatum* Eggers, 1940, Arb. Morph. Taxon. Ent. Berlin 7:139 (Holotype, male?; Trois Rivières, Guadeloupe; Paris Mus.)

When *Hylocurosoma striatum* Eggers, 1940, and *Hexacolus striatus* Eggers, 1934, were both transferred to *Scolytodes*, the species validated in 1940 became a junior homonym. The name *Scolytodes striatulus* is proposed as a replacement name for *Scolytodes striatus* (Eggers, 1940).

### *Scolytodes trispinosus* Eggers

*Scolytodes trispinosus* Eggers, 1934, Ent. Blätt. 30:80 (Holotype, female; Amatán, presumably in Chiapas, Mexico; U.S. Nat. Mus.)

*Scolytodes elongatus* Schedl, 1835, Stylops 4:273 (Holotype, male?; Brazil; Schedl Coll.). *New synonymy*

*Scolytodes trispinosus* Eggers was named from one female labeled Amatán. Subsequently, a hand-written label, "Mexico," was added. This holotype and a female from Brazil compared by me to the type of *Scolytodes elongatus* Schedl were examined. They represent the same species. In all probability this species ultimately will prove to be *laevigatus* Ferrari.

This and allied species are known only from South America. Since the designation "Mexico" was subsequently added to the data borne by the type of *trispinosus*, this species is removed from the Mexican fauna until more substantial evidence of its occurrence in Mexico is found. It apparently breeds in recently fallen *Cecropia* petioles from Colombia to Brazil.

### *Xyleborus costaricensis* Blandford

*Xyleborus costaricensis* Blandford, 1898, Biol. Centr. Amer., Colept. 4(6):210 (Holotype, female; Volcan Irazu, Costa Rica; British Mus. Nat. Hist.)

*Xyleborus nevermanni* Schedl, 1935, Archiv. Inst. Biol. Veg., Río de Janiero 2:93 (Syntypes, female; Vara Blanca, Heredia, Costa Rica; Schedl and Nevermann colls.). *New synonymy*

The female holotype of *Xyleborus costaricensis* Blandford and Schedl's female syntypes of *X. nevermanni* Schedl were both compared directly to my series of 39 specimens from Costa Rica and Panama. Because all of these specimens represent only one species, the name *nevermanni* must be placed in synonymy.

### *Xyleborus improvidus* Schedl

*Xyleborus improvidus* Schedl, 1935, Arch. Inst. Biol. Veg. Río de Janeiro 2:92 (Holotype, female; Moritz, 1858, Venezuela; Schedl Coll.)

*Xyleborus aclinis* Wood, 1974, Brigham Young Univ. Sci. Bull., Biol. Ser. 19(1):38 (Holotype, female; Cerro Punta, Chiriqui, Panama; Wood Coll.). *New synonymy*

The female holotype of *Xyleborus improvidus* Schedl was compared directly to the type series of *aclinis* Wood. All characters agree rather well except for the major tubercles on the declivity. In *aclinis* there are from two to four major tubercles; variation between the four specimens is obvious. The type of *improvidus* bears four tubercles, with a fifth subequal in size at the base of declivital interstriae 2. In view of the variability in *aclinis* and the complete agreement in other characters, it appears that *aclinis* should be placed in synonymy.

### *Xyleborus perforans* (Wollaston)

*Tomicus perforans* Wollaston, 1857, Cat. Coll. Madeira, p. 96 (Syntypes?; Madeira; British Mus. Nat. Hist.)

This species is virtually indistinguishable from *Xyleborus volvulus volvulus* (Fabricius). It tends to average slightly smaller, the declivity is not as steep and less strongly arched, the declivital tubercles average slightly smaller, and the tubercles or crenulations on the ventrolateral margin of the declivity are smaller or obsolete. It occurs abundantly from Australia to India and in parts of Africa, Micronesia, and other areas. Pliocene fossils in amber from northern Kenya clearly are of this species.

In Africa this species now occurs only in limited areas and apparently is being replaced by *v. volvulus* and *v. torquatus* Eichhoff. In Micronesia, most specimens in this complex are of *perforans*, but definite examples of both forms of *volvulus* are present on some islands.

In America, pure series of unquestioned *perforans* have been seen from the USA (Miami, Florida), Costa Rica, and the Antilles Islands. However, several series of both forms of *volvulus* from Peru to Florida contain occasional individuals that appear to be of *perforans* or of a form intermediate between *perforans* and *volvulus*.

Because both "species" appear to have repeatedly moved through commerce and apparently will continue to do so in the future, and because one appears capable of swamping the other through hybridization, I hesitate either to add *perforans* to the American list or to place *perforans* in synonymy until more information is available on what is happening within this complex.

### *Xyleborus spinulosus* Blandford

*Xyleborus spinulosus* Blandford, 1898, Biol. Centr. Amer., Coleopt. 4(6):201 (Syntypes, females; San Geronimo, Zapote, and Mirandilla, Guatemala, Grenada and Guadeloupe; British Mus. Nat. Hist.)

*Xyleborus fusciseriatus* Eggers, 1934, Ent. Blätt. 30:82 (Holotype, female; La Caja, 8 km W San Jose, San Jose, Costa Rica; Berlin Mus.) *New synonymy*

*Xyleborus artespinulosus* Schedl, 1935, Arch. Inst. Biol. Veg. Río Reventazon, Santa Clara, Limon, Costa Rica; Schedl and Nevermann colls.). *New synonymy*

The female syntypes of *Xyleborus spinulosus* Blandford and *X. artespinulosus* Schedl and the holotype of *X. fusciseriatus* Eggers were examined and compared to my series of more than 150 specimens. This common Central American species is quite variable in the size and arrangement of the spines and tubercles on the female elytral declivity. The type specimens of Eggers and Schedl represent only minor variations of *spinulosus* and, for this reason, the names *fusciseriatus* and *artespinulosus* must be placed in synonymy.

## New Taxa

### *Cnemonyx furvescens*, n. sp.

This species is distinguished from *atratus* (Blandford) by the larger size, by the differences in the frons described below, and by the differences in the elytral declivity.

Female.— Length 2.4 mm (paratypes 2.2–2.5 mm), 2.2 times as long as wide; color very dark brown.

Frons as in *atratus* except slightly more elongate, more distinctly, shallowly concave to upper level of eyes, vestiture slightly longer, more abundant.

Pronotum as in *atratus*.

Elytra as in *atratus*, striae more distinctly impressed, punctures on interstriae 2 confused, declivity with striae much less strongly impressed and interstrial granules much smaller, all surfaces more brightly shining.

Male.— Similar to female except frontal vestiture shorter, more uniformly distributed.

Type Locality.— Twenty-seven km NE Montoya, Santander, Colombia.

Type Material.— The female holotype, male allotype, and 21 paratypes (most in poor condition) were taken at the type locality on 2-VII-1970, 150 m, No. 632, *Cespedesia macrophylla*, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

### *Cnemonyx protivorus*, n. sp.

This species is distinguished from *panamensis* (Blandford) by the more coarsely punctured pronotum, by the male frons as described below, and, apparently, by the host.

Male.— Length 2.2 mm (paratypes 2.1–2.5 mm), 2.3 times as long as wide; color almost black.

Frons weakly convex from transverse carina at level of antennal insertion to above eyes; surface subreticulate, punctures moderately course, rather poorly defined; transverse carina acute, occupying median third, smooth and glabrous below carina to epistoma; epistomal margin with a tuft of setae; vestiture above carina about as in *panamensis*, of reddish yellow color.

Pronotum as in *panamensis* except punctures conspicuously larger, particularly in lateral areas.

Elytra as in *panamensis*.

Female.— Similar to male except frons with carina less well developed, smaller, with vestiture shorter, less abundant.

Type Locality.— Forty km SE Socopo, Barinas, Venezuela.

Type Material.— The male holotype and 51 paratypes were taken at the type locality on 25-I-1970, 150 m, No. 256, from *Protium*. The female allotype and 48 paratypes were taken at 17 km SE Miri, Barinas, Venezuela, on 17-XII-1969, 150 m, No. 195, from *Protium*. Other paratypes include 42 from 8 km SE Bumbum, Barinas, Venezuela, 11-II-1970, 150 m, No. 312, from *Protium*. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

### *Cnemonyx squamifer*, n. sp.

This species is distinguished from *splendens* (Wood) by the smaller size, by the smaller, less strongly impressed strial punctures, by the larger, broader interstrial scales, and by the more strongly impressed male frons.

Male.— Length 1.6 mm (paratypes 1.7 mm), 2.2 times as long as wide; color yellowish brown.

Frons similar to *splendens* except more strongly, more broadly concave, vestiture extending slightly above upper level of eyes and closer to margins of eyes.

Pronotum as in *splendens* except punctures conspicuously smaller.

Elytra resembling *splendens* except more weakly impressed, punctures much smaller, very close, interstriae twice as wide as striae, less strongly convex, punctures only slightly smaller than those of striae; interstrial setae in rows, slightly longer and much wider than in *splendens*, each about three to four times as long as wide, about half as long as distance between rows, spaced within a row by length of a seta.

Type Locality.— Tikal, Petén, Guatemala.

Type Material.— The male holotype and two male paratypes were taken at the type locality 13-IV-1956, 100 m, at light.

The holotype and paratypes are in my collection.

### *Cnemonyx visimiacolens*, n. sp.

This species is distinguished from *minusculus* Blandford by the absence of a transverse, subcarinate callus above level of antennal insertion, by the smaller pronotal punctures, and by other characters cited below.

Female.— Length 1.7 mm (paratypes 1.5–1.9 mm), 2.1 times as long as wide; color almost black.

Frons similar to *minusculus* except wider, less strongly impressed, punctures coarser, transverse callus absent or nearly so, vestiture finer, less abundant, mostly shorter.

Pronotum about as in *minusculus* except punctures finer, longitudinal striations finer, more numerous, slightly more extensive.

Elytra similar to *minusculus* except strial punctures less deeply, less distinctly impressed, interstrial punctures smaller, not as deep, not subvulcanate, obscurely granulate on declivity, vestiture usually confined to declivity, mostly abraded.

Male.— Similar to female except frons more distinctly impressed, with vestiture slightly longer, more conspicuous.

Type Locality.— Merida, Merida, Venezuela.

Type Material.— The female holotype, male allotype, and 33 paratypes were taken at the type locality on 22-IX-1969, 1700 m, No. 13, *Vismia* sp. Other paratypes taken in Venezuela include: 17, same data as type except lot 17; 147 from Rancho Grande, Pittier N.P., Aragua 9-IV-1970, 1100 m, No. 432, Guttiferae. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

### *Corthylus nanus*, n. sp.

The unique male is entirely unrelated to known species but is distinguished from *pumilus* Wood by the smaller, more slender form, by the shining, weakly reticulate frons, and by the very different elytra.

Male.— Length 1.2 mm, 2.5 times as long as wide; color reddish brown.

Frons broadly convex, a feeble median granule at epistoma; surface shining, reticulate, very weakly so above upper level of eyes; vestiture fine, inconspicuous.

Pronotum 1.1 times as long as wide; basically as in *minutissimus* Schedl except anterior margin armed only by two slender, contiguous, median serrations; surface reticulate.

Elytra 1.4 times as long as wide, 1.3 times as long as pronotum; sides almost straight and parallel on basal two thirds, rather broadly rounded behind; surface smooth, brightly shining, punctures minute, almost obsolete, perhaps in obscure strial rows. Declivity steep, convex; striae obscurely evident, punctures more distinct than on disc; interstriae 1 weakly, distinctly elevated, 2 strongly, rather narrowly elevated from just below base to just below middle, its narrowly convex crest uniformly elevated, with a row of small punctures, 3 neither elevated nor impressed, with a row of punctures on 1–3 possibly very feebly granulate. Vestiture restricted to declivity, of interstrial rows of subspatulate bristles on all interstriae; about 5–6 on each interstriae, each bristle about one and one-half times as long as distance between rows.

TYPE LOCALITY.— One km southwest of Rincon de Osa, Puntarenas, Costa Rica.

TYPE MATERIAL.— The male holotype was taken on 12-VIII-1968, from a *Cecropia* leaf petiole, by H. Hespenheide.

The holotype is in my collection.

### *Dendrocranulus auctus*, n. sp.

This species is distinguished from *limitaris* Wood by numerous characters cited below.

FEMALE.— Length 1.8 mm (paratypes 2.3–2.7 mm), 2.7 times as long as wide; color very dark reddish brown.

Frons about as in *limitaris* except tuft of hair less dense.

Pronotum as in *limitaris* except posterior areas reticulate, punctures and their accompanying granules much smaller, extending to median area.

Elytra as in *limitaris* except strial and interstrial punctures rather minute, distinctly impressed and declivity rather strongly impressed. Declivity almost smooth, shining, striae obsolete; interstriae 1 slightly elevated, with a row of very fine granules, 2 somewhat strongly impressed, particularly on lower half, with a row of small to feeble granules, 3 higher than 1 and ascending to broadly rounded 4, 3 and 4 each with a row of feeble, minute granules as on 2. Vestiture as in *limitaris* except only two-thirds as long on declivity.

MALE.— Similar to female except frons lesser convex, almost flat on lower half, with rounded tubercles in lateral and dorsal areas, vestiture sparse, declivity much more broadly, strongly impressed (shallowly subconcave), its lateral and apical margins more abruptly rounded, punctures on declivital striae small, distinct, granules slightly larger.

TYPE LOCALITY.— Rancho Grande, Pittier National Park, Aragua, Venezuela.

TYPE MATERIAL.— The female holotype, male allotype, and 48 paratypes were taken at the type locality on 9-IV-1970, 1100 m, No. 407, by me, from the same cucurbitaceous vines that contained *limitaris*.

The holotype, allotype, and paratypes are in my collection.

### *Dendrocranulus limbellus*, n. sp.

The four species in this genus named here (excluding *modus*) are somewhat related to *limbatus* Blandford and *fulgidus* Wood, but all are distinguished by the longer, more slender declivital setae and by the very different arrangement of long frontal setae on the female. The four are allied to one another, but not to other South American members of the genus presently known to me.

FEMALE.— Length 2.4 mm (paratypes 2.0–2.5 mm), 2.9 times as long as wide; color very dark brown.

Frons broadly, evenly convex from epistoma to vertex; surface smooth, shining except obscure reticulation in some lower areas, punctures rather coarse, deep, close on upper half, finer and subgranulate on lower half of area below upper level of eyes; vestiture on lower half of area below eyes of fine, long abundant hair, longest equal to one-third distance between eyes.

Pronotum 1.2 times as long as wide; essentially as in *limbatus* except posterior areas smooth, shining, with no reticulation, punctures distinctly larger, rounded tubercles on lateral margins of most punctures slightly larger.

Elytra 1.7 times as long as wide, 1.6 times as long as pronotum; outline as in *limbatus* except more narrowly rounded behind; disc as in *limbatus* except striae 1 slightly impressed, strial punctures spaced by 1–2 diameters of a puncture, interstrial punctures more widely spaced, declivity narrower, more distinctly impressed on interstriae 2; declivital strial punctures smaller than on disc, interstriae 1 wide, a row of fine, feebly granulate punctures on side next to suture, 2 almost impunctate, 3 with about three fine, rounded granules. Vestiture of interstrial hair, each seta as long as distance between rows, slightly longer toward base of declivity, usually absent on declivital interstriae 2.

Male.— Similar to female except frons almost flat on lower half, with punctures finer, vestiture sparse, declivity much more strongly, more broadly impressed (to middle of interstriae 3), its lateral and apical margins more abruptly rounded.

Type Locality.—Merida, Merida, Venezuela.

Type Material.— The female holotype, male allotype, and 25 paratypes were taken at the type locality on 22-IX-1969, 5300 m, No. 1, from *Cucurbita*, by me.

The holotype, allotype, and paratypes are in my collection.

### *Dendrocranulus limitaris*, n. sp.

This species is distinguished from the very closely allied *limbellus* Wood by the more extensive female frontal vestiture, by the finer punctures on the head, and by differences on the pronotum and elytral declivity cited below.

Female.— Length 2.1 mm (2.0–2.3 mm), 2.7 times as long as wide; color very dark brown.

Frons as in *limbellus* except area above pubescence mostly reticulate, punctures much finer, dense brush of pubescence extending from epistoma to upper level of eyes, longest setae equal to almost half distance between eyes.

Pronotum as in *limbellus* except punctures on disc smaller, their accompanying tubercles larger, tuberculate area extending to median area.

Elytra as in *limbellus* except declivital interstriae 2 ascending laterally, with a row of regularly spaced punctures, granules on interstriae 3 absent, vestiture on declivital interstriae 2 usually present.

Male.— Similar to female except frons less strongly convex (more strongly than male *limbellus*), with vestiture sparse, declivity more distinctly impressed (about as in female *limbellus*), with interstriae 2 largely impunctate, lateral and apical margins broadly rounded.

Type Locality.— Rancho Grande, Pittier National Park, Aragua, Venezuela.

Type Material.— The female holotype, male allotype, and 137 paratypes were taken at the type locality on 9-IV-1970, 1100 m, Nos. 407 (type), 421, 422, 423, from cucurbit vines, by me.

The holotype, allotype, and paratypes are in my collection.

### *Dendrocranulus modus*, n. sp.

This species is distinguished from *carbonarius* (Ferrari) and *guatemalensis* (Hopkins) by characters indicated below.

Female.— Length 1.8 mm (paratypes 1.6–2.0 mm), 2.5 times as long as wide; color very dark brown.

Frons as in *guatemalensis* except weakly, transversely impressed just above epistoma.

Pronotum as in *guatemalensis* except disc less irregular with punctures smaller than in *guatemalensis* but larger than in *carbonarius*.

Elytra as in *guatemalensis* except declivity less strongly impressed (but more so than in *carbonarius*), declivital interstrial setae much longer than in *carbonarius*, slightly longer than *guatemalensis*, each distinctly longer than distance between rows; interstrial punctures on declivity very feebly granulate.

Male.— Similar to female except frons intermediate between males of *guatemalensis* and *carbonarius*, median third on lower half slightly impressed (not impressed in *carbonarius*; in *guatemalensis* impression extends to lateral margins and higher on frons); declivital impression slightly stronger and more extensive than in female.

Type Locality.— Merida, Merida, Venezuela.

Type Material.— The female holotype, male allotype, and 12 paratypes were taken at the type locality on 11-IX-1969, 170 m, No. 1, from *Cucurbita*, by me. Four paratypes are from the same locality, and host, taken 22-IX-1969, No. 18.

The holotype, allotype, and paratypes are in my collection.

### *Dendrocranulus pinguis*, n. sp.

The relationship of this species to *acutus*, *limbellus*, and *limitaris* is more remote. The female frons lacks a dense tuft of hair and the declivity is less distinctly impressed.

Female.— Length 2.4 mm (paratypes 2.2–2.4 mm), 2.5 times as long as wide; color very dark brown.

Frons broadly convex, a weak, transverse impression between eyes; surface reticulate, rather finely, uniformly punctured, lower margins of most punctures shining, perhaps feebly granulate; vestiture sparse, inconspicuous; fine, rather short.

Pronotum 1.2 times as long as wide; resembling *auctus* Wood; disc finely reticulate, punctures very small, distinct, their accompanying tubercles transverse, with longitudinal axis equal to diameter of puncture, transverse axis two or three times as great.

Elytra 1.5 times as long as wide, 1.4 times as long as pronotum; sides straight and parallel on basal two-thirds, slightly tapered then very broadly rounded behind; striae not impressed, punctures moderately coarse, deep, close; interstriae twice as wide as striae, almost smooth, shining, punctures two-thirds as large as those of striae, rather close. Declivity very steep, broadly convex, feebly sulcate on median half; strial punctures slightly smaller than on disc; interstriae 1 slightly elevated, 2 feebly impressed, 3 as high as 1, interstrial punctures almost as large as those of striae, their dorsolateral margins armed by a granule almost equal in height and diameter to puncture. Vestiture abraded on type; on paratypes consisting of erect interstrial bristles, each slightly shorter than distance between rows.

MALE.— Similar to female except frontal impression slightly more extensive, lateral granules larger, declivity more broadly, more strongly impressed (but still rather shallow).

TYPE LOCALITY.— Bumbum Forest Station, Barinas, Venezuela.

TYPE MATERIAL.— The female holotype, male allotype, and six paratypes were taken at the type locality on 29-I-1970, 150 m, No. 276, from a cucurbit vine, by me.

The holotype, allotype, and paratypes are in my collection.

### *Hylocurus clarki*, n. sp.

This species is distinguished from *aberrans* Wood by the more coarsely tuberculate pronotal disc, by the smaller discal strial punctures, and by the very different male elytral declivity.

MALE.— Length 2.3 mm (male paratype 2.5 mm), 2.4 times as long as wide; color dark reddish brown.

Head about as in *aberrans*.

Pronotum as in *aberrans* except disc much more strongly reticulate, rounded tubercles conspicuously larger.

Elytra similar to *aberrans* except strial punctures smaller, interstriae slightly wider than striae and marked by more numerous transverse lines, declivity with spines in circumdeclivital ring blunt, conspicuously more strongly projecting, particularly on upper half, degree of projection about equal to width of spine, punctures of declivital face confused, vestiture on circumdeclivital ring conspicuously longer, more slender, setae on declivital face short, of stout hair.

TYPE LOCALITY.— Between Sicabé and San Miguel Ixtahuacán, San Marcos, Guatemala.

TYPE MATERIAL.— The male holotype and one male paratype were taken at the type locality on 24-II-1972, from *Pinus tenuifolia*, by E. W. Clark.

The holotype and paratype are in my collection.

### *Hylocurus longipennis*, n. sp.

This species is distinguished by the slender body form and by other characters cited below. Though it is more closely allied to *hirtellus* (LeConte) than to other known species, the relationship is not close.

MALE.— Length 2.5 mm (females 2.8–3.0 mm), 3.1 times as long as wide; color very dark brown.

Frons with a strong, transverse carina on more than median half midway between level of antennal insertion and upper margin of eyes; surface concealed by pronotum above carina, smooth, shining, with small punctures at sides and below. Antenna about as in *hirtellus* except club slightly larger, wider, with sutures slightly more strongly procurved.

Pronotum 1.2 times as long as wide; about as in *hirtellus* except disc longer, more strongly reticulate, with subcrenulate tubercles almost twice as large.

Elytra 2.0 times as long as wide, 1.7 times as long as pronotum; sides straight and parallel on basal four-fifths, rather abruptly, serrately tapered to strong, apical mucro; striae not impressed, punctures rather coarse, deep, spaced by diameter of a puncture; interstriae slightly narrower than striae, smooth, shining, punctures small, close, their anterior margins slightly elevated, more strongly so near declivity. Declivity very steep, convex; about as in *hirtellus* except smoother, more brightly shining, tubercles at base slightly larger, broader, interstriae 3 without tubercles below junction with 7, 9 higher and without tubercles on its posterior half; costal margin near apex finely serrate. Vestiture much as in *hirtellus* except interstrial setae at base of declivity longer, coarser, strial setae much shorter.

FEMALE.— Similar to male except frons without a carina, an indefinite callus in its place, upper surface with indefinite punctures and fine, sparse granules, vestiture rather sparse; tubercles at base of declivity finer.

TYPE LOCALITY.— Five km west of El Salto, Durango, Mexico.

TYPE MATERIAL.— The male holotype, female allotype, and two female paratypes were taken on 7-VI-1965, 2500 m, No. 41, from a *Quercus* branch by me.

The holotype, allotype, and paratypes are in my collection.

# ANNUAL ENERGY BUDGETS FOR THREE COMMON RODENT SPECIES IN THE NORTHERN GREAT BASIN[1]

R. Kent Schreiber[2,3]

Abstract.— Annual energy budgets were calculated for three species of small mammals (*Peromyscus maniculatus, Onychomys leucogaster, Reithrodontomys megalotis*) from the northern Great Basin, Benton County, Washington. Individual ingestion rates were based on species activity, microclimate regime, coefficient of digestibility, caloric diet, and the cost for reproduction. For males and females, the estimated energy expenditures were: *P. maniculatus*, 6080, 5891; *O. leucogaster*, 5714, 6587; and *R. megalotis*, 4057, 3791 kcal/yr. By comparison, each species on an individual basis processes more energy annually than the more abundant species in the community, *Perognathus parvus*, but their total contribution to community energy flow is apparently minor. Integration of these results with other ecological parameters is necessary to develop new hypotheses on the role of small mammal consumers in cold desert ecosystems.

Historically, ecologists have studied and compared ecosystems and their component species in terms of density and biomass. However, this approach does not emphasize the impact of each species on the total system or its relationship to other trophic levels within the system. The concept of energy flow provides such a common factor for comparing ecosystems and also for evaluating the relative importance and success of the constituent populations.

In the northern part of the Great Basin common rodent species include the Great Basin pocket mouse (*Perognathus parvus*), deer mouse (*Peromyscus maniculatus*), northern grasshopper mouse (*Onychomys leucogaster*) and the western harvest mouse (*Reithrodontomys megalotis*). These small mammal consumers are representative of an important pathway for energy transfer in a cold desert ecosystem. The bioenergetics of the predominant species, *P. parvus*, has been discussed in a previous paper (Schreiber 1978b). This paper reports on the energy budgets of the three, less abundant, species.

Energy flow through a rodent population can be determined from daily energy requirements and ingestion rates of individuals during each season. In this study I calculated ingestion rates by considering activity of each species in field-encountered microclimates and their resulting metabolic demands. Adjustments in the ingestion rates were made for the additional energy cost of reproduction and for the energy savings while residing in a nest.

## Materials and Methods

### Study Area

The study area is in the Hanford Works Department of Energy (DOE) Reservation 19 km northwest of Richland, Benton County, Washington. The 58-year average annual precipitation for the Reservation is 159 mm. Other climatological and edaphic conditions for the general area have been summarized by Stone, Jenne, and Thorp (1972). Vegetation is mostly typical of the *Artemisia tridentata-Poa* association (Daubenmire 1970) with the exception of native grass species. Cheatgrass (*Bromus tectorum*) was introduced into the area over a half century ago and now has replaced native species as the dominant ground cover. Shrubby species present include big sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and two rabbitbrush species (*Chrysothamnus nauseosus*; *C. viscidiflorus*).

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[1] This study was supported in part by the U.S.-IBP Desert Biome Program (Grant GB 15886 from the National Science Foundation).

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## Trapping

Although no attempt was made in this study to delineate absolute population numbers, monthly sampling with snap-traps determined species composition, relative population sizes, and trends. Traps were spaced approximately 3 m apart, with 50 traps per 150 m line. Rolled oats paste was used for bait and traps were normally set for three consecutive nights in each trapping session. Sex, weight, and reproductive status of all captures were recorded. In addition, rodents were live-trapped in peripheral areas for use in laboratory food trials.

## Microclimate

To establish the microclimate regime of the species, temperatures were recorded continuously at the surface and at a burrow depth of 0.5 m by a seven-day, two-pen thermograph. Data were summarized to coincide with monthly trapping sessions. Mean diurnal surface temperature ($T_d$) was calculated as the average of even-hour temperatures from dawn to dusk. Correspondingly, mean nocturnal surface temperatures ($T_n$) were calculated as the average of even-hour temperatures from dusk to dawn. Burrow temperature ($T_b$) was calculated as the mean of the daily maximum and minimum subsurface temperature.

## Digestibility

Energy content of ingested materials was determined by combustion in a semimicro oxygen bomb calorimeter. The coefficient of digestibility (digested proportion of ingested food) was measured directly in the laboratory from food intake and indirectly by the ash-tracer method for free-living animals (Schreiber 1979).

## Energy Expenditure

Annual ingestion rates were calculated from the activity and resting time of the species in field-encountered microclimates (surface and burrows) and their resulting caloric demands. The additional energy cost of reproduction and the energy savings from insulating properties of the nest were incorporated into the calculations.

Ingestion rates were calculated using the general model:

$$\begin{aligned} I &= [(E_r + E_a) + E_{g_3}]\, D^{-1} \\ &= (E_m + E_{g_3}) D^{-1} \qquad (1) \end{aligned}$$

where I is ingestion rate (kcal/yr), $E_r$ and $E_a$ are energy costs during rest and during activity, $E_m$ is their sum (maintenance), $E_{g_3}$ is energy costs for growth from weaning to subadult, and D is coefficient of digestibility. Additional growth between the subadult and adult stage was considered by using the average adult weight when calculating maintenance energy ($E_m$). During pregnancy and lactation, females incur additional energy demands due to respiration and growth of the embryos. To account for embryonic respiration, gravid females were included in calculations of female mean weight. Ingestion rates for females were calculated as—

$$I_f = (E_m + p\,E_{g_1} + w\,E_{g_2} + E_{g_3})\,(D^{-1}) \qquad (2)$$

—where the coefficient p is mean brood size at parturition (i.e., mean litter size × average number of litters per year), w is the mean brood size at weaning (i.e., mean brood size (p) minus mortality during nursing period), and $E_{g_1}$ and $E_{g_2}$ are energy costs for growth from conception to birth and from birth to weaning, respectively. Intrauterine mortality is unknown but probably small and has been ignored in the calculations. Females with either embryos or placental scars were recorded as bearing one litter; females with both embryos and scars or scars of an undetermined number were recorded as having two litters. For all species I assumed a conservative survival rate of 80 percent for nursing young (Kaczmarski 1966).

*Energy Costs at Rest*: Resting metabolic rates (RMR) for individual species were taken from the literature. Since animals in a burrow and occupying a nest have lower energy requirements during rest, I adjusted RMR's for this energy conservation by plotting the nesting metabolic rate (NMR) as a regression line based on 0.81 RMR at 1 C and 0.87 RMR at 12 C (based on data reported for the harvest mouse, Pearson 1960).

*Energy Cost of Activity*: Metabolic rates increase during periods of activity. Estimates of daily and seasonal variations in amounts of activity were based on field-monitored activity of free-roaming mice tagged with a radioactive nuclide (Schreiber 1973), personal communications from other field investigators, and published data (French et al., 1966). The incremental energy demand ($E_a$) during these activity period was calculated from information cited in Chew and Chew (1970).

*Energy Cost of Growth*: Energy cost for growth during a specific stage of development ($E_g$) is the product of the weight gain (W) and tissue caloric value (K) divided by growth efficiency (G) during that period of growth, i.e.,

$$E_g = (WK)(G^{-1}) \qquad (3)$$

I used the following caloric values for the tissues (K): for the embryo, 0.98 kcal/g fresh weight, based on the average caloric values of five species of newborn rodents (Gorecki 1965, Myrcha and Walkowa 1968, Soholt 1973), and for the unweaned young, 1.39 kcal/g, assuming an average weaning age of 25 days and the mean caloric value of two species of rodents (Myrcha and Walkowa 1968, Soholt 1973). Caloric values for weaned young of individual species are given in the results. Growth efficiencies were taken from the literature and based on average values, G = 13.8 percent for embryos, 15.0 percent for unweaned young, and 5.0 percent for weaned young (Kaczmarski 1966, Migula 1969, Drozdz et al. 1972).

## Results and Discussion

### Composition and Abundance

Snap traps effectively sample small mammal populations (Wiener and Smith 1972), and they are particularly applicable for censusing large areas. Under ideal conditions the total number of individuals caught in traps is proportional to population density and reflects the structure of the population (Hansson 1967, Petticrew and Sadlier 1970). Although trapping percentages are not direct estimates of density, they are nonetheless indicative of population trends and therefore provide insight into the influence a particular species has in the transfer of energy into the community.

Trap lines were operated one night each in September and November 1969 and March, April, and May 1970 and at least three nights per month from June 1970 to May 1971 (Table 1). A total of 1470 rodents was captured in 14,289 trap-days (one trap set for one day). The average monthly effort was 794 trap-days and the overall trapping success was 10.3 percent. Field observations indicated traps placed in dense cover or concealed by shadows had somewhat greater success. On other areas of the Hanford Reservation general trapping success has been reported as low as 4 percent on fire-disturbed grasslands with stony soils (Hedlund et al. 1975) and as high as 44 percent in shrub-steppe habitats with coarse-textured sands (O'Farrell 1975b).

A total of four species of rodents was snap-trapped on the study area: the Great Basin pocket mouse, *Perognathus parvus*; deer mouse, *Peromyscus maniculatus*; northern grasshopper mouse, *Onychomys leucogaster*; and western harvest mouse, *Reithrodontomys megalotis*. *Perognathus parvus* composed 84.2% of the total catch, with *P. maniculatus*, *O. leucogaster*, and *R. megalotis* comprising 9.4, 3.4, and 2.9 percent, respectively (Table 1).

The low trapping success in the fall reflects reduced surface activity and the post-breeding mortality of *P. parvus*, the most abundant species. Summer peaks reflect the termination of reproduction in this species and the increased foraging of weaned young. With the exception of *R. megalotis*, species composition was comparable to small mammal populations inhabiting slightly higher elevations on the reservation, where ground cover consists of more native vegetation (O'Farrell et al. 1975). The greater percent of captures of harvest mice on my study area may reflect this species propensity for habitats with a mixture of native and introduced vegetation (Black and Frischknecht 1971). *Peromyscus maniculatus* was the only species taken throughout the year, although it showed considerable seasonal variation in the number of individuals trapped. *Perognathus* *parvus* was conspicuously absent in the coldest winter months (December and January) and *R. megalotis* was not trapped in the fall months of September and October. *Onychomys leucogaster* was captured each month except February, but trapping success for this species and *R. megalotis* never exceeded 1 percent. Other rodent species, including the sagebrush vole, mountain vole, Townsend's ground squirrel, pocket gopher, and bushy-tailed wood rat occur on parts of the reservation but were absent on my study area.

Because of the unpredictability of precipitation and extremes in temperature, desert rodent populations can demonstrate considerable annual fluctuations. The pocket mouse has specifically adapted to this environment (Schreiber 1978a), and the other species, because of their eurytopic habits, are able to survive at low population levels. Even though total population numbers may exhibit large annual oscillations, the proportional distribution of species probably remains stable over the long term.

## Energy Budgets and Ingestion Rates

Energy flow in the individual is a function of the temperature gradient between body temperature ($T_B$) and ambient temperature ($T_A$). Heat is lost from the body when $T_A < T_B$ and gained by the body when $T_A > T_B$. The rate of metabolism is inversely proportional to the temperature gradient at temperatures below thermoneutrality and directly proportional to temperatures above it. Small rodents, with a relatively large body surface to body weight ratio, gain heat from the environment and dissipation of this heat load against a thermal gradient would require evaporative cooling and subsequent water loss, a luxury desert rodents cannot afford. However, these nocturnal animals rarely encounter ambient temperatures that exceed body temperatures (Table 2), so energy expenditure is mainly from thermogenesis and activity. Females experience additional demands during pregnancy and lactation. Seasonal changes in the insulatory

TABLE 1. Monthly trapping results for the Hanford Study Area, Benton County, Washington.

| | | Species | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | P. parvus | | P. maniculatus | | O. leucogaster | | R. megalotis | |
| Month | Trap days | No. | Trap success (%) | No. | Trap success (%) | No. | Trap success (%) | No. | Trap success (%) |
| *1969* | | | | | | | | | |
| Sep. | 200 | 9 | (4.5) | 1 | (<1) | 0 | | 0 | |
| Nov. | 400 | 17 | (4.2) | 1 | (<1) | 2 | (<1) | 1 | (<1) |
| *1970* | | | | | | | | | |
| Mar.* | 280 | 50 | (17.8) | 6 | (2.0) | 0 | | 1 | (<1) |
| Apr. | 297 | 50 | (16.8) | 13 | (4.4) | 2 | (<1) | 0 | |
| May | 298 | 92 | (30.9) | 10 | (3.3) | 3 | (1.0) | 1 | (<1) |
| June | 2216 | 544 | (24.5) | 39 | (1.7) | 19 | (<1) | 8 | (<1) |
| July | 550 | 166 | (33.2) | 7 | (1.4) | 3 | (<1) | 4 | (<1) |
| Aug. | 450 | 40 | (8.9) | 8 | (1.8) | 4 | (<1) | 1 | (<1) |
| Sep. | 1050 | 48 | (4.6) | 10 | (1.0) | 5 | (<1) | 0 | |
| Oct. | 1648 | 34 | (2.1) | 8 | (<1) | 6 | (<1) | 0 | |
| Nov. | 1300 | 2 | (<1) | 11 | (<1) | 1 | (<1) | 3 | (<1) |
| Dec. | 600 | 0 | | 3 | (<1) | 1 | (<1) | 3 | (<1) |
| *1971* | | | | | | | | | |
| Jan. | 750 | 0 | | 7 | (<1) | 3 | (<1) | 3 | (<1) |
| Feb. | 900 | 3 | (<1) | 6 | (<1) | 0 | | 9 | (1.0) |
| Mar. | 750 | 39 | (5.2) | 3 | (<1) | 1 | (<1) | 4 | (<1) |
| Apr. | 950 | 60 | (6.3) | 4 | (<1) | 0 | | 3 | (<1) |
| May | 750 | 47 | (6.3) | 2 | (<1) | 0 | | 2 | (<1) |
| Aug. | 900 | 37 | (4.1) | 0 | | 0 | | 0 | |
| Total | 14,289 | 1,238 | (8.7) | 139 | (1.0) | 50 | (<1) | 43 | (<1) |

*Heavy rain and strong winds recorded at trapping site properties of the pelage influence metabolic rates, but in small mammals this effect is minimal. Therefore annual energy expenditures of individuals are primarily the result of reproduction.

*Reithrodontomys megalotis*: This rodent was the smallest of the four species captured and it had a scattered distribution on the study area. Although never abundant, it is an opportunist, which enables it to exploit a variety of microhabitats.

Pearson (1960) calculated resting metabolism ($ml\ O_2\ g^{-1}\ hr^{-1}$) in this small cricetid as—

$$E_r = 11.41 - 0.27\ T_b\ (T_b < 24.5\ C) \qquad (4)$$

Adding the increment for activity (2.9 ml $O_2$/g/hr, Chew and Chew, 1970) to $E_r$,

$$E_a = 14.31 - 0.27\ T_A \qquad (5)$$

Harvest mice construct elaborate, well-insulated nests which reduce energy expended for thermoregulation at lower temperatures. Thus,

$$E_n = 9.2 - 0.18\ T_b\ (T_b < 24.5\ C) \qquad (6)$$

Harvest mice may be gregarious during the colder months; if so, their metabolic costs would be effectively reduced. Without nesting material, huddling can reduce metabolic rates 27–39 percent (Pearson 1960, Trojan and Wojciechkowska 1968). With a nest, huddling reduces energy expended in heat production by about 13 percent (Grodzinski and Gorecki 1967) and significantly lowers food consumption (Gebczynska and Gebczynski 1971). I used the latter figure (13 percent) to determine the savings from huddling in a nest.

Although *R. megalotis* is active throughout the year, its surface activity is presumably reduced during the colder months to minimize thermal stress. A male, with a radioactive tag, was monitored for three nights in November (Table 3). The average time spent above ground was 3.3 hours. I accepted this time as representative of both fall and winter activity. This estimate is probably a maximum because individuals may go several days without any surface activity during inclement weather. In fact, both Pearson (1960) and Gaertner (1968) allude to hypometabolism and possible torpor in *Reithrodontomys*. In the spring and summer, food availability and a more energetically favorable microclimate probably extend surface activity. Activity during these seasons was estimated as 4 hours/night, a value also used by Pearson (1960).

Estimated annual energy expenditure for an individual harvest mouse is shown in Table 4. Daily cost for maintenance in males (mean weight 10.76 g) and females (mean weight 9.48 g) is 9.11 and 8.02 kcal, respectively. This amounts to 0.85 kcal/g/day, of which thermoregulation accounts for about 74 percent and activity for 26 percent. Maintenance costs were 25 percent lower in

TABLE 2. Microenvironmental temperatures at the Hanford Study Area.

| | | | Mean temperature, °C | | |
|---|---|---|---|---|---|
| | | | In | At soil surface | |
| Time interval | Length (days) | Midpoint | burrow ($T_b$) | Day ($T_d$) | Night ($T_n$) |
| Jun 17–Jun 28 | 12 | Jun 22 | 24.2 | 43.9 | 22.4 |
| Jun 29–Aug 3 | 36 | Jul 16 | 26.9 | 40.1 | 22.5 |
| Aug 4–Sep 10 | 38 | Aug 22 | 26.0 | 37.0 | 18.5 |
| Sep 11–Oct 12 | 32 | Sep 26 | 19.2 | 21.6 | 8.2 |
| Oct 13–Nov 15 | 34 | Oct 29 | 12.6 | 8.6 | -1.2 |
| Nov 16–Dec 5 | 20 | Nov 25 | 10.6[a] | -1.8[b] | -5.1[b] |
| Dec 6–Jan 1 | 27 | Dec 19 | 8.3[a] | -4.5 | -7.3 |
| Jan 2–Feb 4 | 34 | Jan 18 | 5.6[a] | 0.3 | -4.5 |
| Feb 5–Mar 12 | 36 | Feb 22 | 5.6[a] | 5.2 | -3.6 |
| Mar 13–Apr 11 | 30 | Mar 27 | 10.0 | 18.3 | 2.4 |
| Apr 12–May 11 | 30 | Apr 26 | 16.5 | 29.8 | 11.0 |
| May 12–Jun 16 | 36 | May 29 | 19.7 | 32.2 | 15.7 |

[a] Temperatures taken at 9 dm (Stone, et al., 1972)

[b] Based on 14 days data

TABLE 3. Activity patterns and average amount of time spent on the surface by a male *Reithrodontomys megalotis*.

| Date | Time out | Time in | Elapsed time | Total time* |
|---|---|---|---|---|
| November 27–28 | 21:26 | 23:29 | 2h:03m | 2h:03m |
| | 1:30 | 1:50 | 0h:20m | 0h:20m |
| | 2:43 | 2:54 | 0h:11m | 0h:11m |
| | 3:54 | 4:03 | 0h:09m | 0h:09m |
| | 4:45 | 5:20 | 0h:35m | 0h:35m |
| | 7:08 | 7:33 | 0h:25m | 0h:18m |
| | | | Total | 3h:36m |
| November 28–29 | 21:16 | 22:35 | 1h:19m | 1h:01m |
| | 23:40 | 23:56 | 0h:16m | 0h:16m |
| | 1:50 | 2:10 | 0h:20m | 0h:20m |
| | 3:37 | 3:58 | 0h:21m | 0h:21m |
| | 4:42 | 4:52 | 0h:10m | 0h:10m |
| | 5:47 | 6:12 | 0h:25m | 0h:23m |
| | | | Total | 2h:31m |
| November 29–30 | 20:10 | 21:07 | 0h:57m | Oh:57m |
| | 22:17 | 22:42 | 0h:25m | 0h:25m |
| | 0:24 | 0:50 | 0h:26m | 0h:26m |
| | 3:12 | 4:01 | 0h:49m | 0h:49m |
| | 5:32 | 6:15 | 0h:43m | 0h:43m |
| | 6:47 | 7:07 | 0h:20m | 0h:20m |
| | | | Total | 3h:40m |
| | | | Mean time . . . | 3h:16m |

*Elapsed time minus time for periodic retreats to the burrow

TABLE 4. Annual maintenance energy expenditure for *Reithrodontomys megalotis* at the Hanford Study Area. Body weight: males = 10.76 g, females 9.48 g.

| Time interval | | Hours daily | | Metabolic costs (kcal)[a] | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Dates | Days | At rest | Active | Male | | | Female | | |
| | | | | $E_r$ | $E_a$ | $E_m$ | $E_r$ | $E_a$ | $E_m$ |
| 6/17-6/28 | 12 | 20 | 4 | 62.0 | 20.6 | 82.6 | 54.6 | 18.1 | 72.7 |
| 6/29-8/3 | 36 | 20 | 4 | 159.9 | 62.5 | 222.4 | 140.9 | 55.0 | 195.9 |
| 8/4-9/10 | 38 | 20 | 4 | 172.7 | 73.8 | 246.5 | 152.2 | 65.0 | 217.2 |
| 9/11-10/12 | 32 | 20.7 | 3.3 | 195.0 | 66.5 | 261.5 | 171.1 | 58.6 | 229.7 |
| 10/13-11/15 | 34 | 20.7 | 3.3 | 254.4 | 84.0 | 338.4 | 224.2 | 74.0 | 298.2 |
| 11/16-12/5 | 20 | 20.7 | 3.3 | 156.1 | 52.8 | 208.9 | 137.5 | 46.6 | 184.1 |
| 12/6-1/1 | 27 | 20.7 | 3.3 | 219.4 | 74.9 | 294.3 | 193.3 | 66.0 | 259.3 |
| 1/2-2/4 | 34 | 20.7 | 3.3 | 301.7 | 89.2 | 390.9 | 265.8 | 78.6 | 344.4 |
| 2/5-3/12 | 36 | 20.7 | 3.3 | 319.4 | 92.6 | 412.0 | 281.4 | 81.6 | 363.0 |
| 3/13-4/11 | 30 | 20 | 4 | 229.3 | 84.3 | 313.6 | 202.0 | 74.3 | 276.3 |
| 4/12-5/11 | 30 | 20 | 4 | 195.2 | 70.6 | 265.8 | 172.0 | 62.2 | 234.2 |
| 5/12-6/16 | 36 | 20 | 4 | 212.0 | 75.1 | 287.1 | 186.7 | 66.2 | 252.9 |
| Annual total (Kcal/yr) without huddling | | | | 2477.1 | 846.9 | 3324.0 | 2181.7 | 746.2 | 2927.9 |
| (% $E_m$) | | | | (74.5) | (25.5) | | (74.5) | (25.5) | |
| with huddling | | | | 2289.1 | 846.7 | 3135.8 | 2016.2 | 746.2 | 2762.4 |
| (% $E_m$) | | | | (73.0) | (27.0) | | (73.0) | (27.0) | |

[a] Based on microenvironmental temperatures (Table 2)

the spring and summer than in the fall and winter. For a 9 g individual of this species in central California, Pearson (1960) estimated daily energy costs averaged 7.6 kcal. His lower value reflects both the smaller average weight and the higher microenvironmental temperatures encountered by that population.

The coefficient of digestibility of this species, based on the ash tracer method, was 0.856. After adding the energy cost of preadult growth ($E_{g_3}$), ingestion rate for a male was calculated as:

$$I_m = 3473/0.856 = 4057 \text{ kcal/yr} \qquad (7)$$

Based on a diet of 5.92 kcal/g (mean caloric value of stomach material, Schreiber 1979), a male would consume 686 g per year or about 1.9 g per day.

Weight gains were determined for each growth stage. At birth harvest mice weigh 1.5 g (Svihla 1931). This was increased 0.4 g to account for embryonic tissues. Weaning weight, prorated from that for deer mice, was calculated as 5.4 g. Mean body weight for adult males and nongravid (NG) females was 10.12 g ($N = 34$). Caloric density for adult tissue was 1.58 kcal/g (Schreiber and Johnson 1975); other caloric values and growth efficiencies were given in the methods. Mean litter size (n) was 3.6 ($N = 8$), with females producing 1.11 litters per year (L). The annual ingestion rate for a female was calculated as:

$$I_f = (2928 + 318)/0.856 = 3791 \text{ kcal/yr} \quad (8)$$

These mice expend 16.7 percent of this growth energy between conception and birth, 35.7 percent between birth and weaning, and 47.6 percent after weaning. Females would annually consume 642 g or 1.8 g per day based on the above diet. Huddling during the colder months would reduce total energy expenditure 5.7 percent.

*Peromyscus maniculatus*: Deer mice were the second most abundant rodent in the study area (Table 1). Because this species is also active periodically throughout the year, their activity patterns are presumably similar to those determined for harvest mice. For $E_r$, I adjusted the minimum rate measured by McNab and Morrison (1963, Table 1 and Fig. 3) by 24.5 percent, as suggested by Chew and Chew (1970), to obtain the average resting metabolism:

$$E_r = 9.3 - 0.2\ T_b\ (T_b > 27.1\ C) \qquad (9)$$

Correcting this for the energy used during activity:

$$E_a = 12.2 - 0.2\ T_A \qquad (10)$$

The insulating effects of a nest reduce $E_r$ to:

$$E_n = 7.4 - 0.13\ T_b\ (T_b < 27.1\ C) \qquad (11)$$

Daily, males require about 14.1 kcal and females 12.1 kcal for maintenance (Table 5) or 0.63 kcal/g/day in the spring and summer.

Adding the growth increment and using a coefficient of digestibility of 0.879 calculated for animals living in the wild, the ingestion rate for males was:

$$I_m = 5344/0.879 = 6080 \text{ kcal/yr} \qquad (12)$$

In addition to maintenance costs, females in the study areas produced an average of 1.32 litters per year with a mean number of 4.7 young ($N = 44$). At birth, deer mice weigh an average of 1.8 g (Svihla 1934); embryonic tissues add 1.1 g. Weaning takes place in about 25 days, when animals weigh about 11 g (Svihla 1934, Chew and Chew 1970). Mean adult body weight of males and NG females was 17.5 g ($N = 162$) and adult tissue of this species has a caloric value of 1.56 kcal/g (Schreiber and Johnson 1975). Previously cited values were used for other tissue energy and growth efficiencies. Ingestion rate for females was:

$$I_f = (4425 + 753)/0.879 = 5891 \text{ kcal/yr} \quad (13)$$

Of the 753 kcal used for growth, 16.9 percent was used before birth, 56.1 percent from birth to weaning, and 26.9 percent after weaning. Deer mice on the study area consumed diets with a mean caloric value of 5.75 kcal/ g (Schreiber 1979). Therefore, to meet the required energy demands, males would consume 1.06 kg/yr and females 1.03 kg/yr, or about 2.9 g/day. This amounts to 14.6 percent and 16 percent of the body weight in males and females, respectively. Johnson and Groepper (1970) estimated a 20 g deer mouse in the North Plains consumed 1.9 g of food daily or about 9 percent of its body weight. Deer mice on standard rations at temperatures 10–15 C reportedly consumed an average of 3 g/day (Hatfield, 1940) or 2.8 g/day at 28 C (Sealander 1952).

Energy requirements effecting reproductive stress may substantially increase (e.g., 200 percent) between birth and the end of weaning (Stebbins 1977), so my estimates for females may be somewhat low. Besides huddling, which effectively reduces metabolic costs 5.5 percent (Table 5), deer mice no doubt also resort to additional means of reducing energy expenditure during periods of stress. Marten (1973) found this species may sharply reduce its activity through the summer and activity becomes compressed into the early part of the night, when conditions probably permit a more favorable heat exchange. For the same reason, diurnality may increase in colder months. In winter, pelage (insulation) increases and also contributes to a lower metabolism. Howard (1951) suggested huddling is an important part of energy reduction in deer mice, with torpor occurring in grouped animals. Torpor in this species has also been observed by others (e.g., Morhardt and Hudson 1966, Morhardt 1970). Additionally, Kritzman (1974) and O'Farrell (1975a) suggested possible summer estivation or hypothermia for animals at the Hanford Reservation. Although the rhythmicity of torpor in natural populations is unknown, it could serve both to conserve water in the summer and reduce energy costs at low temperatures or during periods of food scarcity. Hart (1958) also suggested possible alterations in the ability to metabolize food during such periods of stress. As an additional factor, food caches may offer a significant buffer during periods of severe weather and with sufficient stored food, individuals would spend less time on the surface exposed to unfavorable microenvironmental temperatures.

*Peromyscus maniculatus* is omnivorous, demonstrating marked seasonal variation in its diet (Johnson 1964). On other parts of the reservations this species relied heavily on insects for food from spring until fall (Kritzman 1974), probably switching to a more granivorous diet as this food source diminished. It would appear then that competition for available seeds between this species and the more abundant *P. parvus* would be reduced due to their periods of activity, deer mice becoming more dependent on seeds in the colder months when pocket mice are dormant. Additional research is necessary to properly evaluate these aspects of deer mice energetics.

*Onychomys leucogaster*: At an average weight of 25 g, the stout-bodied northern grasshopper mouse was the largest rodent species on the study area. It was present in

Table 5. Annual maintenance energy expenditure for *Peromyscus maniculatus* at the Hanford Study Area. Body weight: males = 19.17 g, females 16.83 g.

| Time interval | | Hours daily | | Metabolic costs (kcal)[a] | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Dates | Days | At rest | Active | Male | | | Female | | |
| | | | | $E_r$ | $E_a$ | $E_m$ | $E_r$ | $E_a$ | $E_m$ |
| 6/17-6/28 | 12 | 20 | 4 | 95.0 | 34.2 | 129.2 | 83.4 | 30.0 | 113.4 |
| 6/29-8/3 | 36 | 20 | 4 | 258.4 | 102.0 | 360.4 | 226.8 | 89.6 | 316.4 |
| 8/4-9/10 | 38 | 20 | 4 | 283.2 | 118.9 | 402.1 | 248.6 | 104.4 | 353.0 |
| 9/11-10/12 | 32 | 20.7 | 3.3 | 301.7 | 102.5 | 504.2 | 264.9 | 90.0 | 354.9 |
| 10/13-11/15 | 34 | 20.7 | 3.3 | 378.2 | 128.5 | 506.7 | 332.0 | 112.8 | 444.8 |
| 11/16-12/5 | 20 | 20.7 | 3.3 | 232.4 | 80.3 | 312.7 | 204.0 | 70.5 | 274.5 |
| 12/6-1/1 | 27 | 20.7 | 3.3 | 329.1 | 111.9 | 441.0 | 289.0 | 98.2 | 387.2 |
| 1/2-2/4 | 34 | 20.7 | 3.3 | 433.9 | 135.2 | 569.1 | 380.9 | 118.7 | 499.6 |
| 2/5-3/12 | 36 | 20.7 | 3.3 | 459.4 | 141.0 | 600.4 | 403.3 | 123.8 | 527.1 |
| 3/13-4/11 | 30 | 20 | 4 | 336.8 | 130.0 | 466.8 | 295.7 | 114.1 | 409.8 |
| 4/12-5/11 | 30 | 20 | 4 | 292.6 | 110.4 | 403.0 | 256.9 | 96.9 | 353.8 |
| 5/12-6/16 | 36 | 20 | 4 | 324.6 | 120.6 | 445.2 | 285.0 | 105.8 | 390.8 |
| Annual total (Kcal/yr) without huddling | | | | 3825.3 | 1315.5 | 5140.8 | 3270.5 | 1154.8 | 4425.3 |
| (% $E_m$) | | | | (74.4) | (25.6) | | (73.9) | (26.1) | |
| with huddling | | | | 3547.8 | 1315.5 | 4863.3 | 3026.9 | 1154.8 | 4181.7 |
| (% $E_m$) | | | | (73.0) | (27.0) | | (72.4) | (27.6) | |

[a] Based on microenvironmental temperatures (Table 2)

low numbers throughout the year. Traps holding these mice were often adjacent to those with mutilated pocket mice, indicating *O. leucogaster's* carnivorous tendency and predatory feeding habits. To my knowledge, no metabolic-temperature function equation presently exists for this species, so I used the equation for *O. torridus* (Chew and Chew 1970), a species of similar size. Average resting metabolism is:

$$E_r = 7.24 - 0.17\,T_b\ (T_b > 27.1\ \mathrm{C}) \qquad (14)$$

This species uses a nest (Ruffer 1965) and, assuming Pearson's (1960) correction for its insulating properties,

$$E_n = 5.86 - 2.12\,T_b\ (T_b < 27.1\ \mathrm{C}) \qquad (15)$$

above-ground activity increases energy expenditure; so,

$$E_a = 10.14 - 0.17\,T_A \qquad (16)$$

presumably, this species has periods of activity similar to harvest mice and deer mice. Annual maintenance costs were estimated as 4857 and 5215 kcal for males and females, respectively (Table 6). Generally, metabolic costs are about 25 percent greater in the colder months than in the warmer months. Nest burrows are shared by male-female pairs (Ruffer 1965); such huddling would produce a 5 percent savings in energy.

Males digest an average of 90.3 percent of their caloric diet. $E_{g_3}$ = 303 kcal for this species, so ingestion rate was calculated as:

$$I_m = 5160/0.903 = 5714\ \mathrm{kcal/yr}\ \text{(without huddling)}$$

or

$$= 4893/0.903 = 5419\ \mathrm{kcal/yr}\ \text{(with huddling)} \qquad (17)$$

Grasshopper mice weigh 2.2 g at birth (Svihla 1936), excluding embryonic tissues (~0.6 g). Females raised an average of 1.07 litters per year with a mean litter of 3.3 young (N = 14). Young are weaned at about 23 days at an average weight of 13.2 g (Pinter 1970) and the mean weight of mature males and NG females was 22.6 g. Using a caloric value of 1.61 kcal/g for adult tissue (Schreiber and Johnson 1975) and other values cited earlier, energy cost for growth from conception to subadult is 660 kcal. The majority of this growth energy is expended after birth. Prenatal growth accounted for 10.6 percent, weaning period for 43.5 percent, and postweaning growth for 45.9 percent. With a digestibility coefficient of 0.892, ingestion rate for females is:

$$I_f = (5215 + 660)/0.892 = 6587\ \mathrm{kcal/yr}\ \text{(without huddling)}$$

or

Table 6. Annual maintenance energy expenditure for *Onychomys leucogaster* at the Hanford Study Area. Body weight: males = 24.3 g, females 26.2 g.

| Time interval | | Hours daily | | Metabolic costs (Kcal)[a] | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Male | | | Female | | |
| Dates | Days | At rest | Active | $E_r$ | $E_a$ | $E_m$ | $E_r$ | $E_a$ | $E_m$ |
| 6/17-6/28 | 12 | 20 | 4 | 82.6 | 35.6 | 118.2 | 89.0 | 38.3 | 127.3 |
| 6/29-8/3 | 36 | 20 | 4 | 219.2 | 105.0 | 324.2 | 236.3 | 113.2 | 349.5 |
| 8/4-9/10 | 38 | 20 | 4 | 239.3 | 124.1 | 363.4 | 258.0 | 133.8 | 371.2 |
| 9/11-10/12 | 32 | 20.7 | 3.3 | 274.3 | 107.2 | 381.5 | 295.7 | 115.5 | 411.2 |
| 10/13-11/15 | 34 | 20.7 | 3.3 | 357.1 | 134.8 | 491.9 | 385.0 | 145.3 | 530.3 |
| 11/16-12/5 | 20 | 20.7 | 3.3 | 222.1 | 83.9 | 306.0 | 239.5 | 90.5 | 330.0 |
| 12/6-1/1 | 27 | 20.7 | 3.3 | 316.2 | 117.4 | 433.6 | 340.9 | 126.6 | 467.5 |
| 1/2-2/4 | 34 | 20.7 | 3.3 | 426.9 | 142.6 | 569.5 | 460.2 | 153.8 | 614.0 |
| 2/5-3/12 | 36 | 20.7 | 3.3 | 452.0 | 147.6 | 599.6 | 487.3 | 159.1 | 646.4 |
| 3/13-4/11 | 30 | 20 | 4 | 325.4 | 135.1 | 460.5 | 350.9 | 145.6 | 495.5 |
| 4/12-5/11 | 30 | 20 | 4 | 272.9 | 115.5 | 388.4 | 294.3 | 124.5 | 418.8 |
| 5/12-6/16 | 36 | 20 | 4 | 293.9 | 126.0 | 419.9 | 316.9 | 135.8 | 452.7 |
| Annual total (Kcal/yr) without huddling | | | | 3481.9 | 1374.8 | 4856.7 | 3733.7 | 1482.0 | 5215.4 |
| (% $E_m$) | | | | (71.7) | (28.3) | | (71.6) | (28.4) | |
| with huddling | | | | 3215.6 | 1374.8 | 4590.4 | 3446.3 | 1482.0 | 4928.3 |
| (% $E_m$) | | | | (70.1) | (29.9) | | (69.9) | (30.1) | |

[a] Based on microenvironmental temperatures (Table 2)

$$(4928 + 660)/0.892 = 6265 \text{ kcal/yr (with huddling)} \qquad (18)$$

Males and females which huddle must daily digest 15.6 (0.69) and 17.2 kcal (0.76 kcal/g), respectively. Diets of grasshopper mice include a variety of insects and seeds plus some animal flesh and green vegetation. Stomach material of this species at Hanford had a mean caloric value of 5.22 kcal/g (Schreiber 1979), about 8 percent lower than the value reported for North Plains individuals (Johnson and Groepper 1970). Based on this caloric diet each male and female in the population studied would annually consume about 1038 g (2.9) and 1200 g (3.3 g/day) of food, respectively. By comparison, in the laboratory on diets of beef liver (72 percent water), grasshopper mice consumed 4.1 g/day (Whitford and Conley 1971).

The incidence of seeds in the diet of this species may significantly increase in the fall and winter (Flake 1971), suggesting it relies on seed caches when insects are less available. Less surface activity would decrease metabolic demands in the colder months. To facilitate this energy savings individuals may restrict more of their winter "hunting" activity to burrow systems. Burrows serve as hibernacula for insects, lizards, and torpid mice, all potential food sources for *O. leucogaster*. The generally high fat deposits of this rodent probably conserve body heat when it is forced to be active on the surface during the cold months.

## Ecological Relationships

Individually, *P. maniculatus* and *O. leucogaster* process between 2½ to 3 times as much energy during the year as *P. parvus*, the most common species (Table 7). The smaller size of the pocket mouse and its periodic use of torpor account for this difference. Based on the relative numbers of individuals (Table 1), however, *P. parvus* dominates as the primary "energy mover" in the small mammal community of this cold desert ecosystem. At the population level, the annual contribution of pocket mice to community energy exchange is nearly 4 times that of deer mice, 11 times that of grasshopper mice, and about 17 times that of harvest mice. Even at high population levels, however, the granivorous pocket mouse does not significantly affect its primary food resource, cheatgrass (Schreiber 1978b). Thus, it is reasonable to assume the euryphagic and less abundant species represented in this paper would also have an insignificant impact on their diverse food resources.

These results additionally refine our understanding of energetics of small mammal com-

TABLE 7. Estimated annual ingestion rates of selected Great Basin rodents.

| Species | Sex | $E_m$[a] (kcal/yr) | Coefficient of digestibility | Mean litter size | Number litters per year | Energy for growth (kcal) | Ingestion rate | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | | (kcal/yr) | (kg/yr)[b] |
| Perognathus[c] parvus | M | 2010 | 0.892 | | | 205 | 2483 | 0.50 |
| | F | 1774 | 0.911 | 3.9 | 1.10 | 360 | 2342 | 0.47 |
| Peromyscus maniculatus | M | 5141 | 0.879 | | | 203 | 6080 | 1.06 |
| | F | 4425 | 0.879 | 4.7 | 1.32 | 753 | 5891 | 1.02 |
| Onychomys leucogaster | M | 4857 | 0.903 | | | 303 | 5714 | 1.09 |
| | F | 5215 | 0.892 | 3.3 | 1.07 | 660 | 6587 | 1.26 |
| Reithrodontomys megalotis | M | 3324 | 0.856 | | | 148 | 4057 | 0.68 |
| | F | 2928 | 0.856 | 3.6 | 1.11 | 318 | 3791 | 0.64 |

[a] Maintenance energy ($E_m$) is calculated without the advantage of savings from hudding.
[b] Based on the mean caloric values of diets of wild mice (Schreiber, 1979)
[c] Taken from Schreiber (1978b)

munities. Unfortunately, the question of the ecological significance of these consumers remains unanswered and a matter of considerable discussion (e.g., Naumov 1975, Chew 1978). As deserts come under increasing pressure for development, the understanding of community function and of the relative cost/benefit of perturbing its various components becomes imperative. Research must now focus on integrating information on bioenergetics with other parameters, such as resource allocation, nutrient cycling and inter- and intraspecific competition, and developing new hypotheses on the role of small mammal consumers.

## Acknowledgments

I am indebted to Dr. Donald R. Johnson, University of Idaho, who initiated this project and secured its financial support. Additional support and facilities were provided by the Joint Center for Graduate Studies and Battelle Pacific Northwest Laboratories, Richland, Washington (USAEC Contract AT(45-1)-2042). The research represents a portion of my dissertation, submitted in partial fulfillment of the requirements for a Doctor of Philosophy degree in zoology from the University of Idaho. Final typing was provided by Sally Vreeland.

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# PRELIMINARY SURVEY OF RAPTOR SPECIES IN THE MANTI DIVISION, MANTI-LA SAL NATIONAL FOREST

Stephen G. Jones[1]

Abstract.— A preliminary survey of raptor species and habitat in the Manti Division, Manti-LaSal National Forest, was conducted during May 1977. Eight species of raptors were recorded, the most common being the Golden Eagle (*Aquila chrysaetos*) and American Kestrel (*Falco sparverius*). Nine additional nesting and migratory species were reported by cooperating observers and based on habitat analysis another two species are expected. Eleven Golden Eagles, representing at least eight pairs, were observed and it is estimated that from 15 to 20 pairs of eagles inhabit the division. The Manti Division provides habitat for two endangered species, the Peregrine Falcon (*Falco peregrinus anatum*) and the Northern Bald Eagle (*Haliaeetus leucocephalus alascanus*). Further research is needed to ascertain the impact that current development activities in the division will have on the raptor community.

With the increased awareness of the critical role that raptors play in balanced ecosystems and the declining nature of many species, land management for the conservation of birds of prey has become an important consideration of governmental agencies administering public lands (White 1974, Olendorff and Kochert 1975). Although U.S. Forest Service lands are administered under the multiple land use philosophy (Griswold, 1978) the conservation of habitat and the protection of areas critical to threatened or endangered species are of prime importance. Paramount to this goal is the identification of species inhabiting an area and assessment of available habitat for species suitability. The present study was conducted to identify the raptor species inhabiting the Manti Division, Manti-LaSal National Forest, and to assess the available habitat for suitability to raptors. This survey takes on added significance because this area is being impacted by the construction and operation of energy-operating facilities. Judgments on critical habitat and the impact of human activity in the division on the raptor community were made but are presented elsewhere (Jones 1977).

## Study Area and Methods

The Manti Division is located in central Utah about 32 km west of Price and extends southward for approximately 120 km (Fig. 1). Elevation ranges from 1,400 to 3,500 m above sea level. The east rim of the Wasatch Plateau forms the eastern boundary of the division. The predominant vegetation types are pinyon-juniper and sagebrush and, at higher elevations, aspen and spruce-fir. Approximately 8 percent of the division is under private ownership. Seven coal mines and four sawmills are operating in or near the national forest.

This study was conducted in the southeastern portion of the Manti Division, encompassing an area of about 960 sq. km. The major canyon systems, the intermittant and permanent streams, and the associated riparian areas provide the habitat used by raptors in the division and were the focal points of this study.

Field work was conducted from 1 May to 15 May 1977. Each of the canyon systems and areas shown in Figure 1 was examined at least once, and in most cases twice. Vehicle travel was possible in all areas except Upper Rocky and Muddy Creek canyons. Raptors were observed and cliff areas examined with 7 × 35 binoculars and a 20X spotting telescope. Data were collected on species seen, nests located, and the suitability of the available cliff, riparian, prey, and roosting habitats present. All nests were delineated on USGS 7½ minute topographic maps for use by Forest Service personnel.

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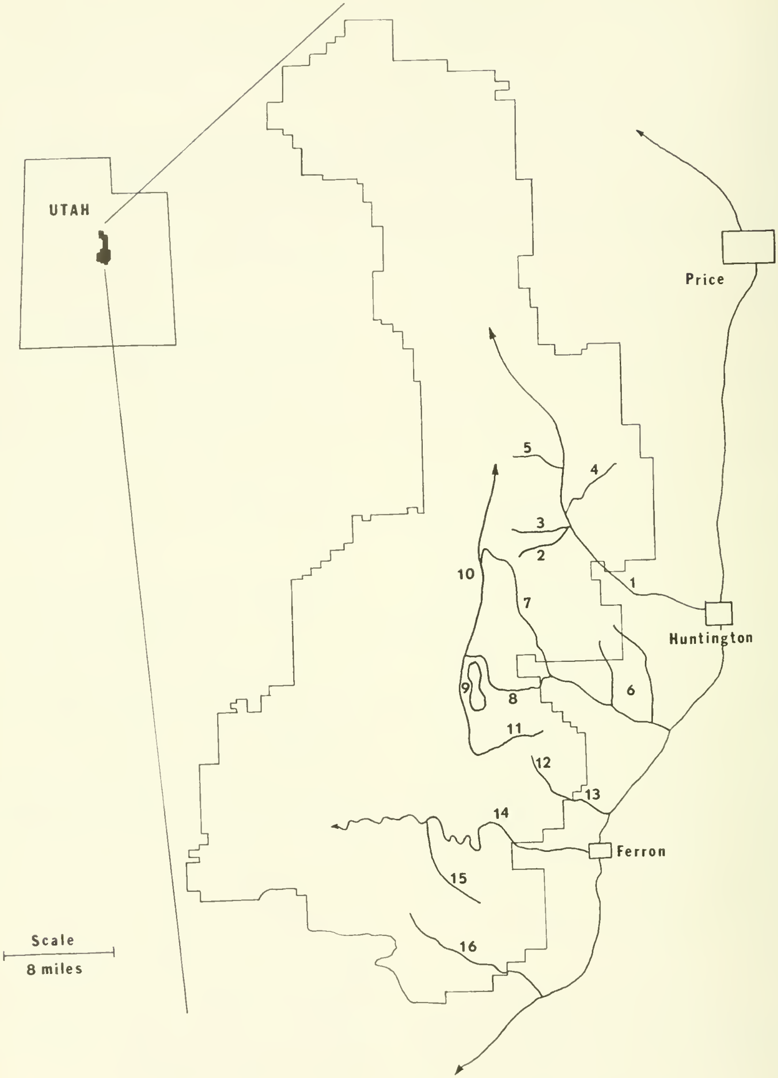
UTAH
Price
Huntington
Ferron
1
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8 miles

Fig. 1. Manti Division, Manti-LaSal National Forest. Numbered areas refer to canyon systems and areas surveyed for raptor species and habitat: 1. Huntington Canyon, 2. Rilda Canyon, 3. Mill Fork Canyon, 4. Tie Fork Canyon, 5. Crandall Canyon, 6. Grimes Wash and Danish Basin, 7. Cottonwood Canyon, 8. Straight canyon, 9. Lower Joes Valley and Lowry Canyon, 10. Upper Joes Valley, 11. North Horn Mountain, 12. Upper Rock Canyon, 13. Lower Rock Canyon including east rim, 14. Ferron Canyon and Bull Hollow, 15. Ferron Canyon overlook and Flagstaff Peak, 16. Muddy Creek Canyon.

The analysis of habitat suitability was based on actual sightings or the probability of use by raptors. Judgments on the probable use of an area were made according to the habitat preferences of each raptor species as described in McGahan (1968), Camenzind (1969), and Beecham and Kochert (1975) for the Golden Eagle (*Aquila chrysaetos*); Porter and White (1974) for the Prairie Falcon (*Falco mexicanus*) and Peregrine Falcon (*F. peregrinus anatum*); Smith and Murphy (1973) and Hayward et al. (1976) for hawks and owls in Utah; Jones (1978) for *Accipiter* hawks and Joseph (1977) for the Northern Bald Eagle (*Haliaeetus leucocephalus alascanus*) wintering in Utah. Judgments about prey habitat were made based on numbers and diversity of potential prey species seen. Special efforts were made to locate eagle nests, as the Golden Eagle is the most sensitive raptor to habitat destruction and disturbance nesting in the division.

## Results

Table 1 presents a list of the eight species of raptor seen and an analysis of the habitat suitability for each of the areas visited. Most commonly seen were Golden Eagles and the American Kestrel (*F. sparverius*), with the Red-tailed Hawk (*Buteo jamaicensis*) and Cooper's Hawk (*Accipiter cooperii*) being seen on several occasions and a Goshawk (*A. gentilis*), Sharp-shinned Hawk (*A. striatus*), and Prairie Falcon each observed once. Great-horned Owl (*Bubo virginianus*) cavities were seen in five areas.

In addition to my sightings, cooperating observers recorded other species of raptors for the division. C. Jemmett, U.S. Forest Service, reports (pers. comm.) occasional Osprey (*Pandion haliaetus*), wintering Bald Eagles, and a Peregrine Falcon in the division. The Ferruginous Hawk (*B. regalis*), Swainson's Hawk (*B. swainsoni*), Turkey Vulture (*Cath-

Table 1. Raptor species seen and habitat suitability in Manti Division, Manti-LaSal National Forest.

| Areas surveyed | Species observed and expected[1] | | | | | | | | | Habitat[3] | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Goshawk | Sharp-shinned | Cooper's | Red-tailed | Golden Eagle | Eagle nest | Prairie Falcon | Kestrel | Owl cavity[2] | Cliff | Riparian | Prey | Roosting[4] |
| 1. Huntington C. | + | – | P | P | – | – | – | + | – | L,I | I | I | – |
| 2. Rilda C. | P | P | – | – | – | – | – | – | – | I | I | I | – |
| 3. Mill Fork C. | P | P | – | P | + | P | – | – | – | I,H | I | I | – |
| 4. Tie Fork C. | P | P | – | P | – | – | – | – | – | I | I | I | – |
| 5. Crandall C. | + | + | + | – | – | – | – | – | – | L | H | I | – |
| 6. Grimes Wash, Danish Basin | – | – | – | – | + | P | – | P | – | L,I | – | H | – |
| 7. Cottonwood C. | P | P | – | P | + | + | – | + | + | I,H | I,H | I,H | – |
| 8. Straight C. | + | – | + | – | + | + | – | + | + | I,H | I,H | I | – |
| 9. Lower Joes Valley, Lowry C. | – | + | – | + | + | + | + | + | + | I,H | I,H | H | H |
| 10. Upper Joes Valley | P | – | – | P | + | P | – | P | – | – | I | H | – |
| 11. North Horn Mtn. | – | – | – | – | + | – | – | + | – | – | – | H | – |
| 12. Upper Rock C. | – | – | – | – | + | + | – | P | – | I,H | – | L,I | – |
| 13. Lower Rock C., East Rim | – | – | – | – | + | – | – | – | + | L,I | – | L,I | – |
| 14. Ferron C., Bull Hollow | – | – | P | – | + | P | – | + | – | L,I | I,H | I,H | H |
| 15. Ferron C., Flagstaff Peak | P | – | – | + | – | – | – | P | + | L,I | – | I | – |
| 16. Muddy Creek C. | – | – | + | – | – | – | – | P | – | L,I | I | I | – |

1. Species and structures: + = Observed, – = Not observed, P = Probable occurrence.
2. Cavities assumed used by Great-horned Owls.
3. Habitat suitability: L = Low, I = Intermediate, H = High
4. Roosting habitat suitability judged with respect to wintering Bald Eagles.

*artes aura*), Marsh Hawk (*Circus cyaneus*), Saw-whet Owl (*Aegolius acadicus*), and Flammulated Owl (*Otus flammeolus*) have been recorded by Phil Wagner, Division of Wildlife Resources (pers. comm.). However, several of these species inhabit the division only during migration. Based on habitat analysis and distribution accounts in Behle and Perry (1975) and Hayward et al. (1976), another two species, the Screech Owl (*O. asio*) and Pygmy Owl (*Glaucidium gnoma*), should also occur in the Manti Division.

Eleven Golden Eagles, representing at least eight pairs, were seen within nine areas. The eagle sighted on North Horn Mountain is believed to nest in Upper Rock Canyon. Seven eagle nests were found within four areas; centers of these nesting areas were from 6.4 to 12.8 km apart. Approximate home range sizes for the eagles in the division can thus be calculated as 44 to 132 sq. km, assuming a roughly circular territory (see Smith and Murphy 1973).

Goshawks, Sharp-shinned, and Cooper's hawks appear to be rather common residents in the Manti Division. Suitable riparian habitat in most areas was occupied or suspected to be occupied by at least one of the three species. Typically, the Cooper's Hawk will select the lower elevations with more open habitat, with the Goshawk and Sharp-shinned Hawk nesting higher up and accepting steep canyons. Crandall Canyon supported all three species. Due to the secretive nature of these hawks, observations are uncommon even in areas where they are nesting.

Red-tailed Hawks should occur more commonly in the division than the few actual sightings would indicate. They are suspected of nesting on many of the same cliffs that the eagles were using. During winter the Red-tailed Hawk is the most commonly seen hawk in the division (P. Wagner, pers. comm.).

The sighting of the Prairie Falcon in Lower Joes Valley is the first record of this species for the division (C. Jemmett, pers. comm.). Suitable nesting areas for Prairie Falcons were found in Lower Joes Valley and Cottonwood Canyon. The individual sighted is believed to nest in the canyons west of Lower Joes Valley.

Where seen, Kestrels were numerous. In Lower Joes Valley at least six pairs showed nesting activity during this study. The only habitats not supporting Kestrels were the dry sagebrush areas and the steep mountain canyons.

Cavities suspected of being used by Great-horned Owls were seen in five different areas. Great-horned Owls should be widely distributed in the Manti Division. Nesting cavities do not always show signs of usage, and crow or hawk nests are often used by owls. The other species of owls recorded or suspected are also thought to be widely distributed in the division.

A correlation from Table 1 of species presence and habitat availability is indicative of the rather restricted habitat preference of *Accipiter* hawks and the general preference of eagles, Red-tailed Hawks, and Kestrels. The dry mountainous habitat of the Manti Division will support a certain assemblage of breeding raptors, but other species will be restricted. Ultimately, habitat availability and climatic regimes are responsible for the avian species living in an area. In the Manti Division steep-sided canyons occupied by Accipiter hawks open into sloping sagebrush valleys or high aspen meadows that are utilized by eagles, Red-tailed Hawks, and Kestrels. Little falcon habitat is available, except in Lower Joes Valley. The higher elevations restrict such lower desert species as the Ferruginous Hawk.

## Discussion

The Manti Division supports a high diversity of raptors, with as many as 17 species utilizing the division during the breeding season and on migration. This study provides an estimation of the breeding raptors within the area surveyed. Wagner (unpubl. ms.) provides data on the raptors utilizing the division during migration. On 1–2 September 1977 a count of migrating raptors along the Manti Mountain-Skyline Drive yielded the following numbers for each species: Turkey Vulture—5, Goshawk—1, Cooper's Hawk—3, Sharp-shinned Hawk—1, Red-tailed Hawk—66, Swainson's Hawk—1, Ferruginous Hawk—1, Golden Eagle—4, Kestrel—43, Prairie Falcon—2 and Marsh Hawk—3 (total = 130). This list is similar to the breeding list with the exception of the relative numbers of each species.

Wintering Bald Eagles will utilize Lower Joes Valley reservoir and should also be present in Ferron Canyon. C. Jemmett reports (pers. comm.) that Bald Eagles stay at Lower Joes Valley reservoir as long as waterfowl are present on the reservoir. In severe winters the reservoir and stream freeze over by January and are not used by wintering eagles. Important characteristics of areas used by wintering Bald Eagles are permanent streams which do not freeze over, riparian type vegetation with a high degree of exposure, and the presence of migrating waterfowl, rabbits, or an abundance of local fishes as prey species (Joseph 1977).

The density of nesting Golden Eagles found on the Manti Division is similar to that found in other western states. McGahan (1968) found the maximum area used by eagles in Montana was from 180 to 205 sq. km. Dixon (1937) reports the area used by 27 nesting pairs in the California foothills ranged from 52 to 160 sq. km. Assuming that eagles are distributed evenly over the entire Manti Division and using the value of 80 sq. km to represent their approximate habitat size requirements, the division should support from 15 to 20 pairs. Considering the number of eagles observed during this rather limited study, the above estimate seems conservative. Nesting densities of eagles in central Utah can, however, vary greatly between years, with cyclic fluctuations in prey densities (Camenzind 1969, Murphy 1975).

Analysis of habitat suitability for raptors shows that relatively few areas in the division provide habitat for all species, or complete habitat for any one species (Table 1). The notable exceptions to this are Crandall Canyon, Cottonwood Canyon, Lower Joes Valley, and Ferron Canyon; these areas provide both nesting and foraging habitat for three to six species. More typically, however, suitable nesting habitat is found in one area and foraging habitat in another area. For example, North Horn Mountain may be used for foraging by as many as three pairs of Golden Eagles, but on the mountain proper there is no eagle nesting habitat.

In addition to the utilization of the habitat within the division by an endangered species, the Bald Eagle, and a sighting of a second endangered species, the Peregrine Falcon, several of the other resident raptors, are experiencing population declines in other areas of the United States. The need for protection of populations of these species is, therefore, critical. Important in this is an understanding of the ecology of each species of raptor involved, including its breeding requirements, nesting habits, and foraging and food habits. Further research on the raptors in the Manti Division is recommended so that current development activities do not threaten the species now utilizing the area. Murphy (1978) outlines management techniques for the western raptors which would be applicable for the Manti Division. Schamberger and Farner (1978) discuss the process of using habitat evaluations in project planning, which is also applicable. The raptors in the Manti Division represent a valuable natural resource, as important for ecological, scientific, and aesthetic reasons as energy resources and recreational potential are for economic reasons.

## Acknowledgments

Support for this study was provided by the Manti-LaSal National Forest, Contract Q-77-4. Mr. Coy Jemmett, wildlife biologist, Manti-LaSal National Forest, Price, Utah, organized the study and provided administrative assistance. I wish to acknowledge Anita Jorgensen for her assistance during field work.

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# VEGETATION RESPONSE TO A MOISTURE GRADIENT ON AN EPHEMERAL STREAM IN CENTRAL ARIZONA

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ABSTRACT.— Ecological aspects of desert vegetation in relation to a moisture gradient along an ephemeral stream in central Arizona were investigated. The stream channel, flood plain, and north-, west-, south-, east-facing slopes represent a moisture gradient going from mesic to xeric conditions. Vegetation in some areas of the stream channel intergraded into flood plain vegetation, which in turn intergraded into slope vegetation types. In other areas there were sharp delineations between stream channel and flood plain and between flood plain and slope. Trees and legume species preferred midmoisture habitats, but forbs, shrubs, and succulents preferred dryer areas. Family groups like the Asteraceae and the Poaceae were found to be distributed ubiquitously. Niche widths were broadest for flood plain species. Diversity was highest on the slopes. Negative correlations existed between stand diversity and the Synthetic Stand Moisture Index (i.e., as moisture increased diversity increased). It is believed that disturbance as well as moisture influenced diversity.

Central and southern Arizona are considered to be part of the Sonoran Desert, which occupies much of the southwestern United States and northern Mexico. Physiographically, the area is characterized by small mountain ranges rising above level basins and by a vegetation comprised of shrubs, small trees, cacti, and associated ephemerals. The level basins are now liberally marked by arroyos or wadis (i.e., dry washes cut by the action of ephemeral streams). Bryan (1928) suggests that the arroyo cutting is of recent origin.

The rainfall pattern of the Sonoran Desert exhibits two distinct peaks: (1) a summer rainy period from July to September characterized by thunder storms of short duration and heavy rainfall intensity, and (2) the gentle rains of December through March caused by the southward movement of subtropical high pressure systems. Summer rains which are of greater intensity vary less from year to year than do the winter rains (Mallery 1936a). Localized storms in the region are very pronounced, often being limited to a few square miles.

Temperatures in the Sonoran Desert are characterized by great diurnal fluctuations, hot summers and warm winters. Freezing temperatures may occur, but without regularity and they do not last for extended periods of time.

Vegetational descriptions of the Sonoran Desert in part at least include Nichol (1952), Whittaker and Niering (1964, 1965), Marks (1950), Glendening and Paulsen (1955), Little (1950), Kramer (1962), Richards (1925), and Shreve (1922, 1924). Spalding (1910), Blumer (1909, 1910) and Walmo (1955) briefly mention desert vegetation in foothill sites they studied in the southern Arizona mountain ranges. Keil (1970) and Letho (1970) recently completed floristic studies in two areas of the Sonoran Desert located in Maricopa County.

Ecological studies dealing with isolated fragments of Sonoran Desert ecosystems are more numerous than are those dealing with community dynamics or entire community structure. For example, germination studies of annuals (Klikoff 1966, Capon and Asdell 1967, Beatley 1967, Went 1942, 1948, and 1949, Went and Westgaard 1949, Juhren et al. 1956, and Trevis 1958a, 1958b) and of perennials (Turner 1963, Shreve 1931, Turner et al. 1966, and Barbour 1968) have been done. Productivity studies of perennials (Chew and Chew 1965) and their ecology in relation to soil types, mineral nutrients, water

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relations, and plant associations (Yang 1950, Livington 1910, Yang 1957, Gardener 1951, 1959, Spalding 1909, Yang and Lowe 1956, Rich 1961, Reynolds 1962, Muller and Muller 1956, Dalton 1962, Wilm 1956, Parker and Martin 1952, Reynolds and Tshirley 1957, and Halvorson and Patten 1974) have also attracted interest. Work with climatic factors in desert areas has been completed by Smith (1956), Sellers (1960), Humphrey (1933), and Mallery (1936a, 1936b). Niering et al. (1963), Turner (1963), and Halvorson (1970) have briefly discussed the pattern of vegetational change from mountain slopes down onto the basin floors. However, their discussions are limited to population dynamics and vegetation studies of foothills and mountain slopes.

Halvorson (1970) indicates that the valleys and mountains of central Arizona have not been studied in detail as is the case with the mountain and foothill areas in the more southern portions of the state (see Whittaker and Niering 1964, 1965, Niering et al. 1963, Spalding 1909, 1910). The purpose of this study was to describe the vegetational zonation patterns existent along an ephemeral stream in central Arizona and to determine whether the observable vegatational patterns represented a continuum adapted to a moisture gradient from slope to stream channel or if they represented distinct, discrete communities.

## STUDY AREA

The study area lies in a foothill region of the Sonoran Desert and is part of the Mexican Highlands, a subdivision of the Basin and Range Province, which is geographically located to the west and south of the Colorado Plateau (Halvorson 1970).

The area of study is a five-mile section of New River, an ephemeral stream located 35 miles north of Phoenix, Arizona (Fig. 1). This section of the river parallels Interstate 17 for 2.5 miles and then bends away following Table Mountain and paralleling Table Mesa Road (Fig. 1). New River is a tributary of the

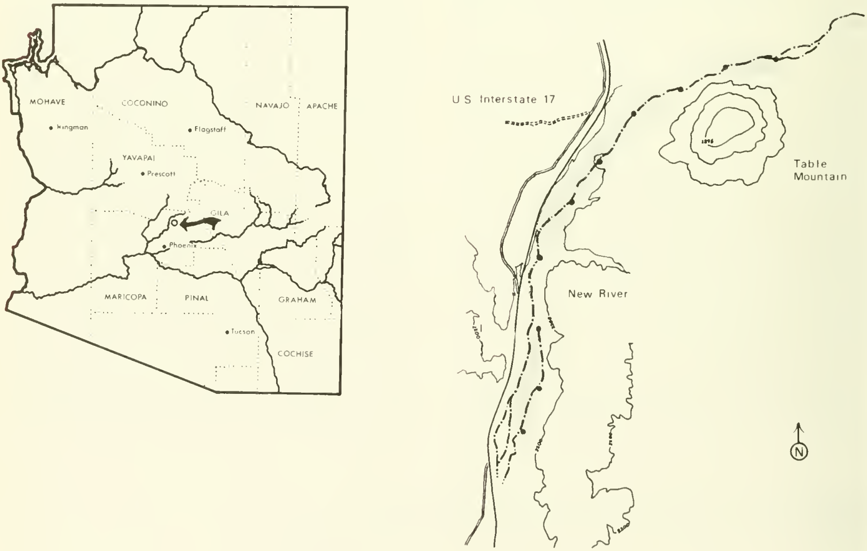


Fig. 1. Map of the study area showing location in Arizona.

Agua Fria River, which feeds into the Gila river and drains most of Central Arizona.

Metamorphic, igneous, and sedimentary rock comprise the parent material through which the Gila River and its tributaries flow. Davis (1925) proposed the origin of the existing mountain ranges to be tilted and moderately dissected fault blocks. From such ranges the broad desert basins have derived their soil, collected from alluvial material eroded from adjacent mountain slopes. The soils in the study area are generally shallow and poorly developed. Desert pavement is a prominent feature in the area and, as is the case in many desert areas, a narrow surface horizon exists in association with a caliche near the soil surface. The area has been subjected to grazing by domestic livestock since the 1800s. Location 2 of the study area is in close proximity to the site of an old stage station. Much of the area is now controlled by the Tee Cattle Company.

## Methods

Ten study sites were located at one-half-mile intervals along a five-mile section of New River (Fig. 1). Five stands were selected at each site, one stand each at the following locations: both slopes adjacent to the stream channel, the flood plain on both sides of the stream channel, and the stream channel itself. In each stand, three 5 × 10 m plots were set up approximately 3 m apart. Four quadrats, each 1 m square, were placed inside each large plot. Trees and treelike vegetation were sampled within the large plots, and small shrubs, forbs, and grasses were sampled using the meter square quadrats. Frequency data were taken and used in the analysis.

Vegetation patterns were analyzed through the use of a synthetic moisture gradient. The moisture gradient was established through knowledge gained from the literature (Niering et al. 1963) and from work done in the field. The stream channel was selected as being the most moist. The two flood plain units were lumped together and considered the next most moist. In most north temperate floristic systems, the north-facing slopes are considered to be more moist than the opposite south-facing slopes (Daubinmire 1974). Such considerations are generally attributed to a shadowing effect of the hills and mountains that prevent direct sunlight from ever reaching the area. A similar relationship has been noted with east- and west-facing slopes. However, because of the peculiar shadowing effect of the adjacent hills noted in the study area, it was felt that the east-facing slope would exhibit the dryest conditions, with the west-facing slope fitting in between the north- and south-facing slopes on the moisture gradient. Those stands common to each area (i.e., stream channel, floodplain, etc.) were lumped together and average frequency values for each species in the area were computed. The species were then arranged in order of their occurrence in the six areas (Table 1). Those species most frequent in the stream channel were segregated to the top of the table and those most frequent on the east-facing slope were placed near the bottom, with all others falling somewhere in between. From this table indicator species were selected using as a basis frequency values approximately twice that in one group as in any other. The indicator species were then weighted with an index number. The index number was determined as follows: the stream channel species, selected as being representative of the most moist areas, were assigned the index number 5; the flood plain species in the next most moist area were assigned the number 4; and so on with the species of the east-facing slope receiving the number 0. When the frequency value of a species was not twice that of the next highest group, yet was greater and formed the apex of an increased upward trend, the species was assigned an index number midway between those for the groups in which the two largest frequencies were found and included as an indicator.

Synthetic Stand Moisture Index values (SSMI), similar to Plot Index Values (PIV) described by Dix and Butler (1960), were constructed by dividing the sum of the composite indices for all indicator species found in a stand by the sum of the stand frequencies of those indicator species found in that stand. The composite index values were determined by multiplying the stand frequency of an indicator species by its moisture index number. Therefore,

$$\text{SSMI} = \frac{\Sigma \text{ composite index values for indicator species}}{\Sigma \text{ frequency values for indicator species}}$$

SSMI values were computed for all stands. The stands were then placed along a one-dimensional ordination in an attempt to relate the stands spatially. Indicator species and other vegetational parameters were then graphed against the ordination in an attempt to elucidate trends. Average frequency values were computed for all stands falling between the SSMI values of 0 to 1, 1 to 2, 2 to 3, 3 to 4, 4 to 5, on the moisture gradient. This method was employed because it showed trends much more clearly than the entering of all points.

Cluster analysis techniques (Sneath and Sokal 1963) were applied to similarity index figures obtained by utilizing Sorenson's index of similarity (Sorensen 1948) and the following equation from Dix and Butler (1960):

$$K = \frac{2W}{a + b} \times 100$$

TABLE 1. Average percent frequency values for species distributed in the six groups used to establish the synthetic stand moisture gradient. Numbers to the left of the species names represent index numbers assigned to those species selected as indicator species of the different groups.

| | | Average percent frequency | | | | | |
|---|---|---|---|---|---|---|---|
| | | River bottom | Flood-plain | Slope | | | |
| | Species | | | North | West | South | East |
| 5 | *Baccharis glutinosa* | 83 | 33 | 0 | 0 | 0 | 0 |
| 4.5 | *Baccharis sarothroides* | 55 | 33 | 0 | 0 | 0 | 0 |
| 4.5 | *Hymenoclea monogyra* | 45.5 | 35.4 | 0 | 0 | 0 | 0 |
| 5 | *Salix* sp. | 33 2 | 0 | 0 | 0 | 0 | 0 |
| 4.5 | *Polypogon monspeliensis* | 25 | 14.6 | 0 | 0 | 0 | 0 |
| 5 | *Euphobia* sp. | 19.5 | 8.3 | 0 | 0 | 0 | 0 |
| | *Bromus rubens* | 16.7 | 15.9 | 12.5 | 0 | 0 | 8.3 |
| 4.5 | *Minulus glabratus* | 10.4 | 8.3 | 0 | 0 | 0 | 0 |
| 4.5 | *Datura meteloides* | 8.3 | 8.3 | 0 | 0 | 0 | 0 |
| | *Marrubium vulgare* | 0 | 8.3 | 0 | 0 | 0 | 8.3 |
| | *Mammillaria microcarpa* | 0 | 8.3 | 0 | 8.3 | 0 | 8.3 |
| 4.5 | *Avena fatua* | 0 | 8.3 | 0 | 0 | 0 | 0 |
| 3 | *Ephedra viridis* | 0 | 8.3 | 8.3 | 8.3 | 0 | 0 |
| | *Lepidium* sp. | 8.3 | 13.9 | 8.3 | 0 | 0 | 0 |
| 4 | *Franseria ambrosioides* | 0 | 19.8 | 0 | 0 | 0 | 0 |
| 4.5 | *Cynodon dactylon* | 16.5 | 25.2 | 0 | 0 | 0 | 0 |
| 4 | *Platanus wrightii* | 0 | 33 | 0 | 0 | 0 | 0 |
| | *Lycium fremontii* | 0 | 53.7 | 33 | 44.3 | 33 | 33 |
| | *Acacia greggii* | 0 | 62.2 | 0 | 66.7 | 0 | 0 |
| | *Prosopis juliflora* | 33 | 76.1 | 49.5 | 66.7 | 58 | 61 |
| | *Simmondsia chinensis* | 0 | 55 | 69.8 | 58.5 | 33.2 | 66.2 |
| | *Cercidium microphyllum* | 0 | 49.6 | 66.5 | 46.5 | 58 | 58 |
| | *Schismus barbatus* | 13.8 | 37 | 56.2 | 19.4 | 30.2 | 41.5 |
| 2.5 | *Ferocactus wislizeni* | 0 | 8.3 | 33 | 37.1 | 8.3 | 8.3 |
| 2.5 | *Eriogonum fasciculatum* | 0 | 0 | 38.8 | 33.3 | 8.3 | 0 |
| | *Larrea divaricata* | 0 | 43.3 | 49.5 | 49.5 | 0 | 51.4 |
| 1 | *Eriogonum* sp. | 0 | 0 | 0 | 0 | 25 | 8.3 |
| | *Plantago purshii* | 0 | 26.1 | 16.7 | 32 | 38.9 | 33.2 |
| 1 | *Opuntia leptocaulis* | 0 | 0 | 0 | 8.3 | 58.3 | 16.7 |
| | *Opuntia engelmannii* | 0 | 16.7 | 0 | 26.8 | 66.7 | 20.6 |
| | *Opuntia bigelovii* | 0 | 33 | 55.5 | 66 | 82.5 | 52.1 |
| 1.5 | *Fouquieria splendens* | 0 | 0 | 55.6 | 66 | 100 | 0 |
| | *Salsola kali* | 0 | 0 | 0 | 0 | 0 | 16.6 |
| 0.5 | *Enchinocereus engelmanii* | 0 | 8.3 | 0 | 8.3 | 16.7 | 24.9 |
| | *Carnegiea gigantea* | 0 | 40.3 | 0 | 33 | 33 | 49.5 |
| 0 | *Opuntia fulgida* | 0 | 33 | 0 | 33 | 33 | 66.5 |
| 1 | *Franseria deltoidea* | 0 | 30.1 | 8.3 | 59.7 | 56.5 | 80.0 |

where "K" equals the index of similarity, "a" is the frequency of all species in one stand, "b" is a similar figure for a second stand, and "W" is that part held in common by both stands.

Analyses of the similarity index values and the cluster techniques were carried out on an IBM 7030 computer.

Niche width and stand diversity values were computed using the equation $B = 1/\Sigma pi^2$ where "B" is equal to either the niche width and/or diversity and "pi" is a measure of the relative abundance of a species in a given habitat (Levins 1966, MacArthur 1972). Niche width values for a species were obtained by summing its pi values across all stands. Diversity values, on the other hand, were computed by summing the pi values for all species found, in a single stand.

The P × F (Presence × Frequency) index (Anderson 1964, Curtis 1959) was computed for all species found in the study area to give an indication as to species importance in the system (Table 4).

Diversity Indices (DI) were compared to the SSMI by regression analysis (Hall 1971, Dick 1971) to determine if any relationship existed between the two measures. Species determinations follow Kearney and Peebles (1951).

## RESULTS AND DISCUSSION

The five-mile section of New River presents a study in contrasts. Characteristically the flood plain tends to be wide in some areas and narrow in others. The vegetation along the wide areas intergrades readily with that of adjacent slopes, but sharp lines of demarcation appear between flood plain and slope vegetation where the flood plain narrows. The flood plain exhibits a wide variety of vegetational pattern. The broader areas display vegetation types closely allied to those of adjacent slopes, with the narrow areas exhibiting greater densities of trees, shrubs, and thicket-forming plants. The river channel itself is wide, sparsely vegetated, and disturbed periodically by high water flow resulting from heavy rains in the mountains, evidenced by the highly sorted sand, gravel, and rocky nature of the channel substrate. Seep areas in the channel are characterized by the presence of water nearly year-round. In these areas larger trees such as *Salix spp.* and *Platanus wrightii* are found along with *Mimulus glabratus* and *Baccharis gulutinosa*. The north-, west-, south-, and east-facing slopes in that sequence appear to be in order of decreasing moisture. Differences in ground cover, the number, and types of individuals on the slopes is apparent. The north-facing slopes generally exhibit a larger more mesophytic flora.

Vegetation analysis involved establishing a synthetic moisture gradient. This was accomplished by arranging species in order of moisture delineations and assigning index numbers (Table 1). Synthetic Stand Moisture Index values (SSMI) were then computed for all stands (Table 2). Using these values the stands were placed on a one-dimensional ordination along the proposed moisture gradient, which oriented them spatially to each other (Fig. 2). Average frequency for indicator species and life form groups in all stands were then graphed against the one-dimensional ordination.

Species and life form groups were found to peak in importance along sections of the gradient (Figs. 3–4). *Franseria deltoidea*, for example, is well adapted to the dryest moisture regime on the gradient, but *Baccharis sarothroides* occurs in more moist sites. Figure 3 also depicts the relationships of several of the indicator species (i.e. *Fouquieria splendens, Ferocactus wislizeni*, and *Cercidium microphyllum*), for those stands of the study area occurring between 1 and 2 on the moisture gradient. Other species exhibiting similar patterns to those in Figure 3 were *Opuntia leptocaulis, O. bigelovii, O. engelmannii*, and *Plantago purshii* (Table 1). Also shown are the patterns exhibited by index plants (i.e., *Franseria deltoidea, Opuntia fulgida*, etc.) of the gradient class, 0 to 1. Species showing similar patterns were *Salsola kali* and *Carnegiea gigantea*. The species *Hymenoclea monogyra* and *Cynodon dactylon* showed peak prefence in the most moist areas (Fig. 3). *Baccharis glutinosa, Salix spp., Euphorbia spp., Mimulus glabratus*, and *Dature meteloides* are other species found to exhibit similar patterns. *Franseria ambrosioides* (Fig. 3) peaked between the SSMI values of 3 and 4, which represents the flood plain area of the study. Other species prefering this same habitat were *Acacia greggii* and *Simmondsia chinensis*. It should be noted, however, that these two species are rather ubiquitous and may be prominent in other areas as well. *Schismus barbatus* and *Eriogonum fasciculatum*, though not clear-cut index plants of the west and south slopes (there were no clear-cut indicators for this section of the gradient), show optimum frequency peaks in this area.

Because the relationship between various

Table 2. Stands listed along with their Synthetic Stand Moisture Index values (SSMI), diversity indicies, aspect and/or topographic position on the landscape. EF = east facing slope, SF = south facing slope, WF = west facing slope, NF = north facing slope, FP = floop plain, and SC = stream channel.

| | | | Diversity | | | | Diversity |
|---|---|---|---|---|---|---|---|
| Stand No. | SSMI | Location° | Index | Stand No. | SSMi | Location | Index |
| 1 | 1.0 | EF | 5.886 | 25 | 4.5 | RB | 3.019 |
| 2 | 1.0 | EF | 4.970 | 26 | 4.5 | RB | 2.062 |
| 3 | .91 | Ef | 5.394 | 27 | 0 | RB | 0 |
| 4 | 0 | EF | 4.003 | 28 | 4.6 | RB | 2.538 |
| 5 | .50 | EF | 6.270 | 29 | 4.7 | RB | 3.019 |
| 6 | .83 | EF | 9.452 | 30 | 4.6 | RB | 3.331 |
| 7 | 1.0 | SF | 5.388 | 31 | 4.5 | FP | 5.160 |
| 8 | 1.3 | SF | 5.504 | 32 | 4.2 | FP | 1.790 |
| 9 | 1.0 | SF | 6.515 | 33 | .90 | FP | 7.457 |
| 10 | .67 | SF | 9.050 | 34 | 2.2 | FP | 9.461 |
| 11 | 1.0 | FP | 4.988 | 35 | 4.5 | FP | 7.530 |
| 12 | 2.8 | FP | 5.643 | 36 | 2.9 | FP | 2.173 |
| 13 | 2.8 | FP | 7.348 | 37 | 3.9 | FP | 4.137 |
| 14 | 4.1 | FP | 4.160 | 38 | .90 | FP | 6.357 |
| 15 | 1.0 | FP | 8.446 | 38 | 5.0 | FP | 4.798 |
| 16 | 1.2 | FP | 6.826 | 40 | 1.0 | WF | 7.819 |
| 17 | 2.1 | FP | 6.506 | 41 | 1.0 | WF | 8.184 |
| 18 | 3.6 | FP | 4.653 | 42 | 1.0 | WF | 5.063 |
| 19 | 4.4 | FP | 4.909 | 43 | 1.0 | WF | 5.131 |
| 20 | 0 | FP | 3.266 | 44 | 1.0 | WF | 2.507 |
| 21 | 4.8 | SC | 6.400 | 45 | 1.8 | WF | 6.053 |
| 22 | 4.8 | SC | 3.263 | 46 | 1.6 | NF | 6.169 |
| 23 | 4.5 | SC | 3.693 | 47 | 1.2 | NF | 6.105 |
| 24 | 4.6 | SC | 4.602 | 48 | 1.6 | NF | 3.949 |
| | | | | 49 | .50 | NF | 5.385 |

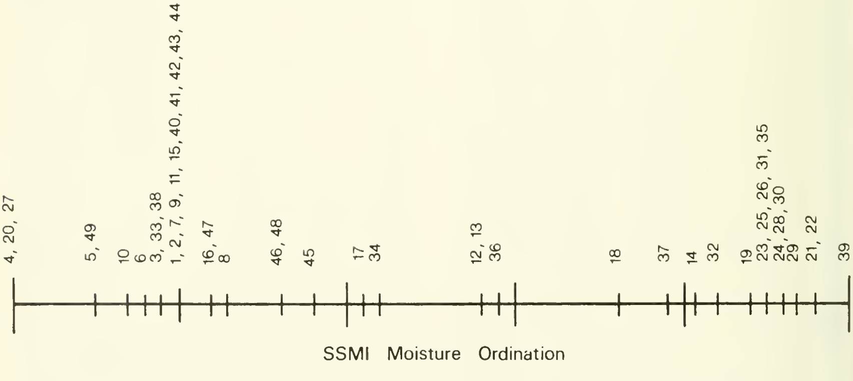


Fig. 2. One-dimensional ordination by SSMI values of stands along the moisture gradient.

life form groups and the moisture gradient was of interest, six groups were chosen—i.e., shrubs, succulents (cacti and cactuslike plants), trees, woody plants, forbs, and selected plant families (i.e., composites and legumes). Figure 4 shows great similarity between the established pattern for trees and that of legumes. It should be noted that the number of species these two groups had in common was high. Of further interest is the fact that the two groups contain species characteristic of the north-facing slope and of me-

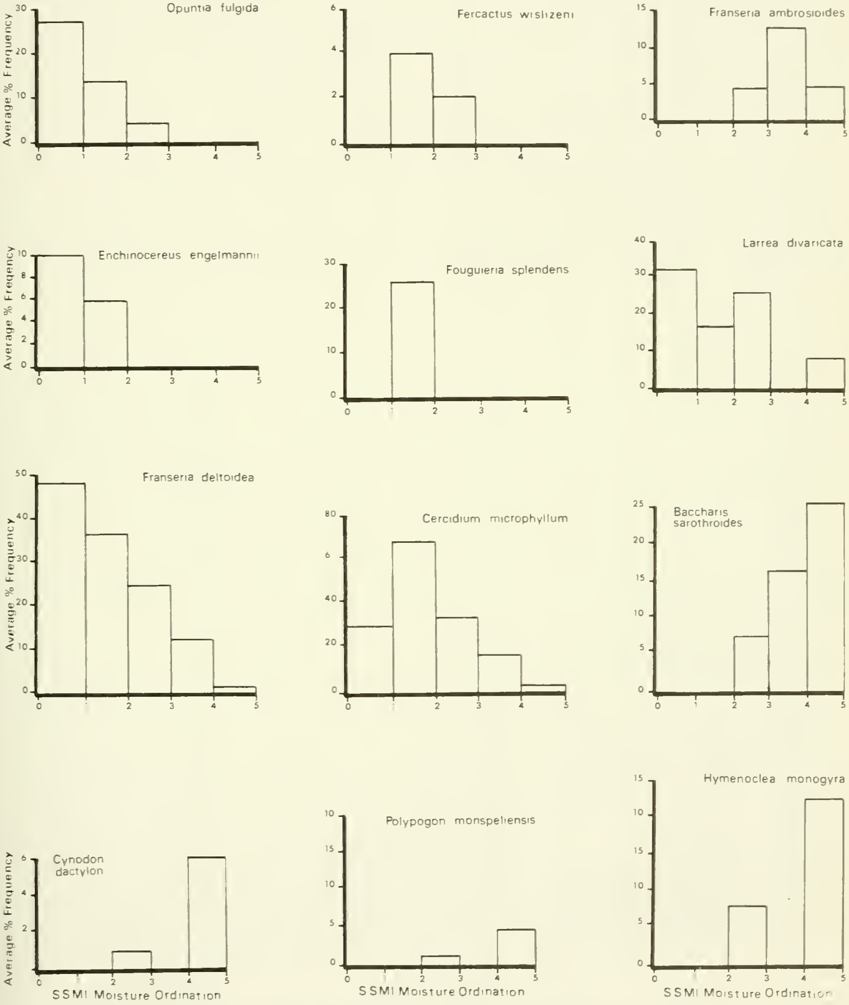


Fig. 3. Average percent frequency for indicator species plotted against the moisture gradient.

dium moisture regime preference. The shrubs, succulents, forbs, and woody plants as groups (Fig. 4) tend to prefer the dryer moisture habitats. The composites (as well as other family groups such as the grasses) showed no preference for particular sections of the moisture gradient and exhibited, as groups, rather ubiquitous distribution patterns in relationship to the SSMI gradient.

When cluster analysis techniques were applied to the 37 species (Fig. 5), five major groups were apparent; however, a few species did not relate well to any group. From left to right on the dendrogram the groups are: (1) predominately flood plain and lower bajada species, which include *Acacia greggii*, *Larrea divaricata*, *Schismus barbatus*, *Cercidium microphyllum*, and *Carnegiea gigantea*; (2) north- and west-facing slope species, which include *Fouguieria splendens* and *Eriogonum fasciculatum*; (3) south- and east-facing slope species, which include *Enchinocereus Engelmannii* and *Opuntia leptocaulis*; (4) flood plain species, which include *Bromus rubens* and *Franseria ambrosioides*; and (5) the stream channel species *Cynodon dactylon*, *Salix spp.*, and *Hymenoclea monogyra*. The relationships of these five groups to the established moisture gradient are depicted in Figure 6. As can be seen, all sections of the proposed moisture gradient are represented.

When the dendrogram (Fig. 7) for the 49 stands was constructed, five groups were again recognized. Table 3 indicates how these groups relate with regard to the topography of the study area. From the cluster analysis it appears that the west-, south-, and east-facing slopes were highly similar in vegetation types, and that those stands which were subjectively picked as being similar at the beginning of the study are in fact grouped together by cluster analysis. This

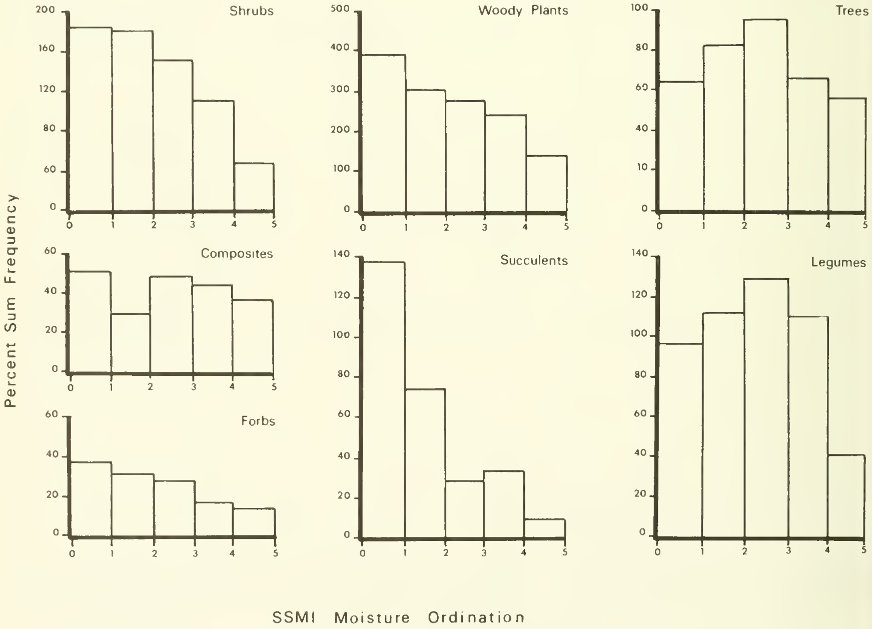


Fig. 4. Average percent frequency of life form groups plotted against the moisture gradient.

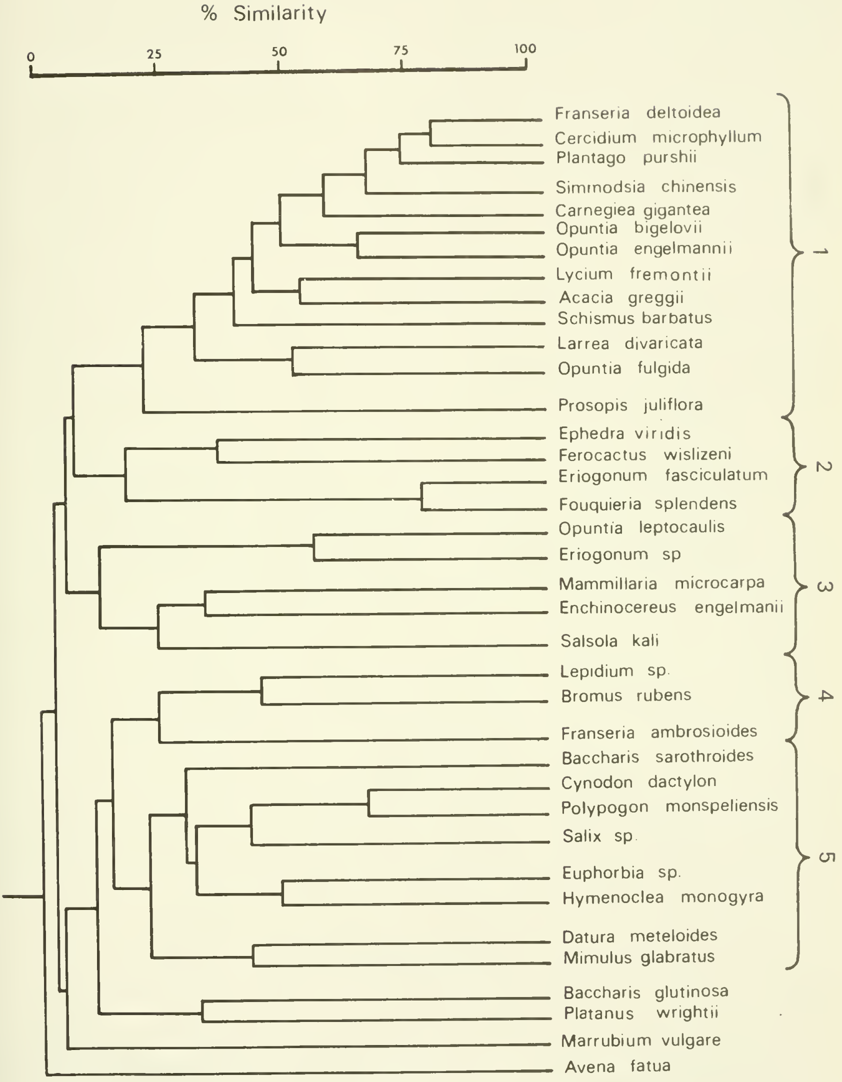


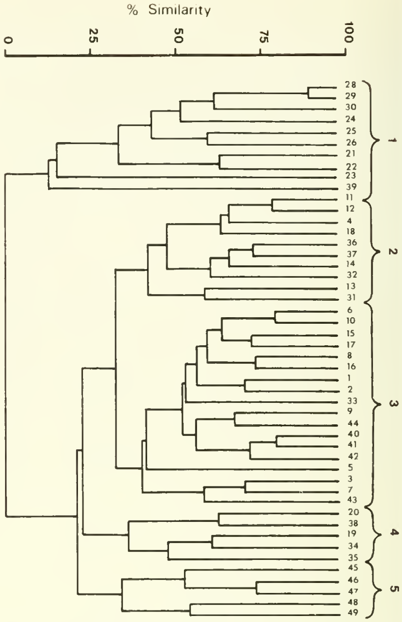
Fig. 5. Dendrogram of "cluster" analysis of 37 species.

would, of course, be expected if one assumes that the vegetation of an area reflects the general pattern of its abiotic environment (Niering et al. 1963).

Figure 8 illustrates niche width relationships to moisture preference. Flood plain species exhibit the broadest niche widths when compared with slope and stream channel species. Cluster analysis (Fig. 5) grouped species with similar niche widths together. Table 4 ranks all species in order of decreasing niche width and further serves to illustrate the point that those species with the broadest

Table 3. Dendrogram groups as designated in Figure 7, along with included stands and their predominant aspect and/or topographical location.

| Dendrogram Group # | Stand # | Predominant location |
|---|---|---|
| 1 | 21, 22, 23, 24, 25, 26, 28, 29, 30, 39 | River channel |
| 2 | 4, 11, 12, 13, 14, 18, 31, 32, 36, 37 | Floodplain |
| 3 | 1, 2, 3, 5, 6, 7, 8, 9, 10, 15, 16, 17, 33, 40, 41, 42, 43, 44 | Slopes (east, south, west) |
| 4 | 20, 38, 19, 34, 35 | Floodplain |
| 5 | 45, 46, 47, 48, 49 | North-facing slope |


% Similarity
0
25
50
75
100
28
29
30
24
25
26
21
22
23
39
11
12
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18
36
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32
13
31
6
10
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17
8
16
1
2
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41
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3
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20
38
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49
1
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Fig. 7. Dendrogram of "cluster" analysis of 49 study plots.

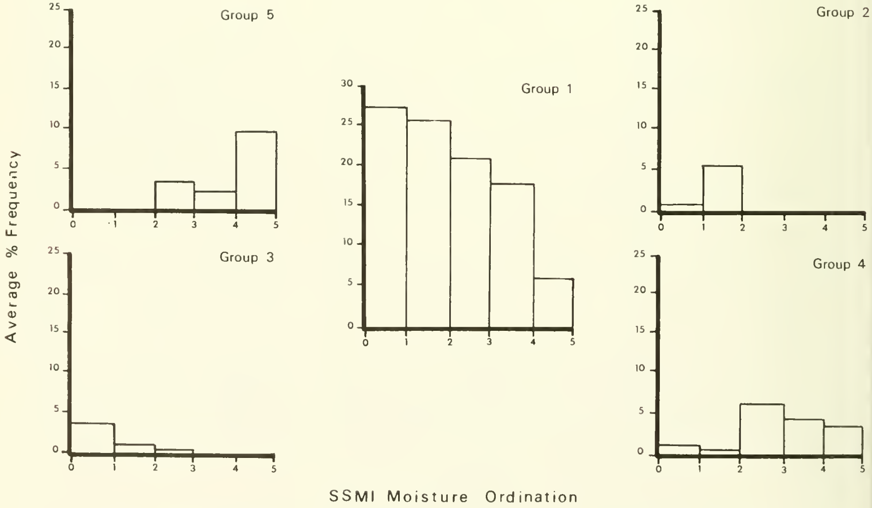

Fig. 6. Average frequency of cluster group species plotted against the inferred moisture gradient.

niches are, generally speaking, flood plain species. As indicated earlier, the flood plain includes a wide variety of habitats and it may be this fact that influences the broadest niches being noted in the flood plain.

Table 5 gives figures for the means ($\bar{x}$) and standard deviations for NW, SSMI, and DI figures. Regression analyses indicated that the NW vs. SSMI values exhibited highly significant correlations ($p < .001$). When niche

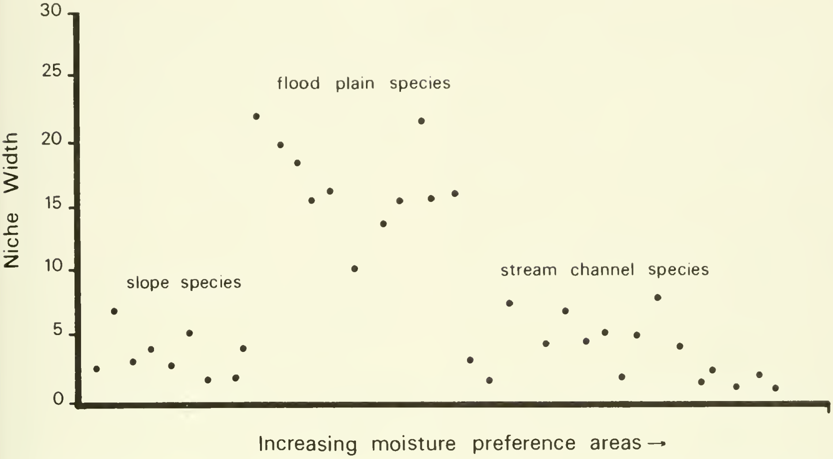

Fig. 8. Average diversity index values and average niche width values plotted against the moisture gradient.

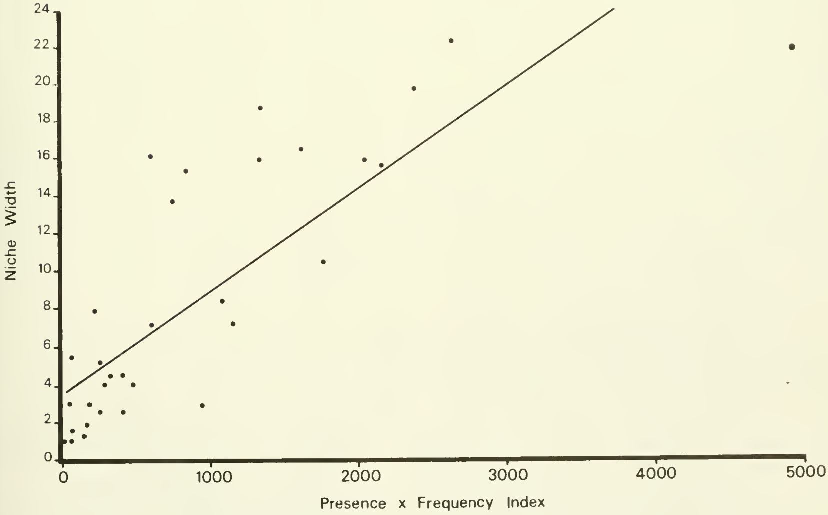

Fig. 9. Regression analysis of the relationship of NW vs. P × F index.

width measurements were compared by regression analysis to the P × F index values (Table 4 and Fig. 9), the relationship was again highly significant ($p < .001$) with an $r^2$ value of .68. It appears that the two parameters generally express similar information in terms of species importance in a community.

The relationship of the Diversity Index (DI) parameter to stand placement along the moisture gradient is illustrated in Fig. 10. As

TABLE 4. List of species encountered in the study, along with their niche width, percent presence, average percent frequency, and presence times frequency (P×F) index. Species are ordered in decreasing value of niche width.

| Species | Niche width | Percent presence | Average frequency | P×F index |
|---|---|---|---|---|
| *Acacia greggii* | 22.359 | 73.5 | 67.4 | 4954 |
| *Franseria deltoidea* | 22.293 | 57.1 | 45.9 | 2620 |
| *Cercidium microphyllum* | 19.724 | 42.9 | 55.2 | 2368 |
| *Plantago purshii* | 18.720 | 49.0 | 27.4 | 1343 |
| *Carnegiea gigantea* | 16.529 | 38.3 | 41.7 | 1618 |
| *Bromus rubens* | 16.152 | 42.9 | 13.9 | 596 |
| *Schismus barbatus* | 15.962 | 46.9 | 28.6 | 1341 |
| *Larrea divaricata* | 15.949 | 36.7 | 55.2 | 2044 |
| *Simmondsia chinensis* | 15.657 | 30.6 | 70.6 | 2160 |
| *Lycium fremontii* | 15.314 | 32.7 | 25.4 | 831 |
| *Opuntia engelmannii* | 13.648 | 18.4 | 40.3 | 742 |
| *Opuntia begelovii* | 10.483 | 28.6 | 61.6 | 1742 |
| *Hymenoclea monogyra* | 8.389 | 22.4 | 48.1 | 1077 |
| *Lepidium* sp. | 7.886 | 20.4 | 10.8 | 220 |
| *Prosopis juliflora* | 7.227 | 18.4 | 62.7 | 1154 |
| *Baccharis sacrothroides* | 7.184 | 14.3 | 42.4 | 606 |
| *Fouquieria splendens* | 5.450 | 8.2 | 57.8 | 66 |
| *Polypogon monspeliensis* | 5.391 | 18.4 | 18.5 | 340 |
| *Euphorbia* sp. | 5.181 | 14.3 | 17.8 | 225 |
| *Cynodon dactylon* | 4.518 | 18.4 | 22.2 | 408 |
| *Franseria ambrosioides* | 4.466 | 16.3 | 19.6 | 319 |
| *Mammillaria microcarpa* | 4.000 | 8.2 | 57.8 | 474 |
| *Ferocactus wislizeni* | 4.000 | 14.3 | 20.1 | 287 |
| *Datura meteloides* | 4.000 | 6.1 | 8.3 | 51 |
| *Ephedra viridis* | 3.006 | 6.1 | 8.3 | 51 |
| *Enchinocereus engelmannii* | 2.986 | 12.2 | 15.6 | 190 |
| *Opuntia fulgida* | 2.910 | 20.4 | 46.3 | 945 |
| *Baccharis glutinosa* | 2.575 | 6.1 | 66.5 | 404 |
| *Eriogonum fasciculatum* | 2.571 | 8.2 | 31.2 | 256 |
| *Marrubium vulgare* | 2.000 | 4.1 | 8.3 | 34 |
| *Opuntia leptocaulis* | 1.853 | 6.1 | 27.7 | 169 |
| *Eriogonum* sp. | 1.579 | 4.1 | 16.7 | 68 |
| *Salsola kali* | 1.577 | 4.1 | 16.7 | 68 |
| *Mimulus glabratus* | 1.293 | 16.3 | 9.4 | 153 |
| *Avena fatua* | 1.000 | 2.0 | 8.3 | 17 |
| *Salix* sp. | 1.000 | 2.0 | 33.0 | 66 |
| *Platanus wrightii* | 1.000 | 2.0 | 33.0 | 66 |

TABLE 5. Mean (X) and standard deviation (SD) values for the diversity indices (DI), synthetic stand moisture indices (SSMI), and niche widths (NW) as computed for stands grouped in cluster analysis (Figure 7 and Table 3).

| | DI | | SSMI | | NW | |
|---|---|---|---|---|---|---|
| Groups° | X | SD | X | SD | X | SD |
| 1 | 3.67 | 1.27 | 4.25 | 1.18 | 8.36 | 5.82 |
| 2 | 4.58 | 1.74 | 2.98 | 1.46 | 13.90 | 6.84 |
| 3 | 6.47 | 1.73 | 1.02 | .31 | 14.98 | 6.44 |
| 4 | 6.30 | 2.35 | 2.40 | 2.03 | 12.48 | 6.32 |
| 5 | 5.54 | .97 | 1.34 | .52 | 11.69 | 7.41 |

opposed to niche widths, stand diversity was highest in the bajada and slope stands. In tropical ecosystems high uniformity is positively correlated with high diversity (MacArthur and Wilson 1967). However, in north temperate systems this relationship appears to be reversed—i.e., low uniformity yields high diversity (Dick 1971, Hall 1971). The data from our study seem to follow a similar pattern. There are, however, other parameters not measured in this study (i.e., disturbance as indicated by the presence of the introduced species *Avena fatua* and *Bromus rubens*, etc.) which, it is felt, have influenced the diversity trends of the area.

## Conclusions

It is apparent that the stream channel has a set of species (among which are *Polypogon monspeliensis, Datura meteloides, Baccharis glutinosa*) distinct in many ways from those in the other areas; yet all are clearly a part of an integrated system. For example, *Bromus rubens, Cercidium microphyllum,* and *Acacia greggii* grow not only in the stream channel but also on the flood plain and slopes. The flood plain is highly varied in habitat, resulting in a mosaic of types. Some of the stream channel vegetation intergrades only into the flood plain, and the flood plain vegetation in turn intergrades into slope vegetation, especially where the plain is wide. In some locations where it is narrow the change between flood plain and channel vegetation or between flood plain and slope plain is sharply delineated, so that one can easily delineate channel food plain or slope vegetation. In other areas the flood plain is broad and the change from channel to flood plain to slope is so gradual and smooth that one is hard put to find where the stream channel ends and the flood plain begins. Due to the wide variety in habitats on the flood plain those species that are found to be ubiquitous throughout the flood plain region exhibit the broadest niche. Such species (i.e., *Acacia greggii, Cercidium microphyllum, Larrea divaricata*) with broad niche widths were predominately species of importance in the flood plain and lower bajada. Where the slope is distinct from the flood plain, it is clearly more sparsely vegetated than the flood plain and is dominated by several small shrubs. *Franseria deltoidea* is most prominent in these areas. In still other locations there exists a mixture of many species wherein no one species distinctly dominated.

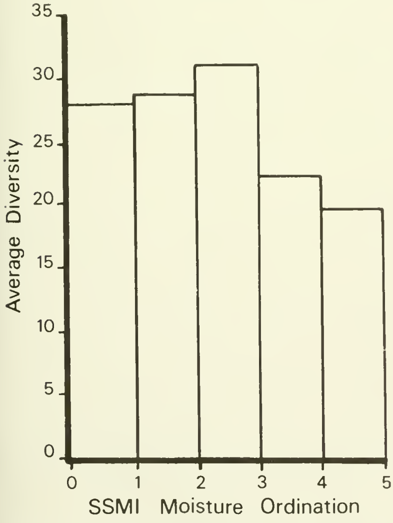

Fig. 10. Niche width (NW) plotted against species arranged by dendrogram sequence.

Species of similar life forms and taxa often showed similar location preference. Family groups in general, however, were ubiquitous and everywhere present. For example, the composites, as a family, are probably the most prevalent group in the study area and showed no identifiable trends. Other prominent families are the Poaceae and the Fabaceae. The grasses, though ubiquitous in distribution, showed no decided location preference. The legumes, on the other hand, appear to prefer medium moisture areas. With many of the legumes being trees or treelike forms, the arbrorescent life form also exhibited medium moisture preferences. Surprisingly, the forbs preferred the dryer moisture areas; however, this may be due to factors other than moisture. Succulents which are predominately cacti preferred the dryer moisture regimes. *Carnegiea gigantea*, one of the more prominent cacti on the area, exhibited its highest frequency value on the slopes. It did, however, extend onto the flood plain in some locations. Shrubs, as a group, represented by species like *Franseria deltoidea*, *Larrea divaricata*, and *Franseria ambrosioides* also preferred the dryest moisture areas.

Cluster analysis results were useful in that they substantiated many assumptions of the initial hypothesis which were subjectively stated. Species when clustered together exhibited similar niche widths and were also observed to occupy habitats in similar topographical locations. Stands when clustered produced groups which correlated to all sections of the moisture gradient. This evidenced that the gradient (though synthetically constructed) did, in fact, reflect natural conditions. Six different areas were established and delineated as distinct (i.e., stream channel, flood plain, north-, west-, south-, and east-facing slopes). Cluster analysis indicated distinctness in the flood plain, stream channel, and north-facing slope stands, but clustering west-, south-, and east-facing slope stands were as one unit. Vegetatively speaking, these three areas were highly similar and support vegetation distinctly different from the other three locations.

The patterns exhibited when indicator species frequency values were plotted against the moisture gradient also substantiate that the established moisture gradient is realistic and that the indicator species chosen are good index plants of general moisture conditions.

The relationships noted between the P × F index and the niche width measurements indicate that the two express similar information in terms of species importance in a system. Their correlation to each other is positive and highly significant.

Diversity was shown to be highest on the slopes and negatively correlated to moisture (i.e., as moisture increases diversity decreases) (Fig. 11). It is felt, however, that the diversity data would have been more meaningfully in-

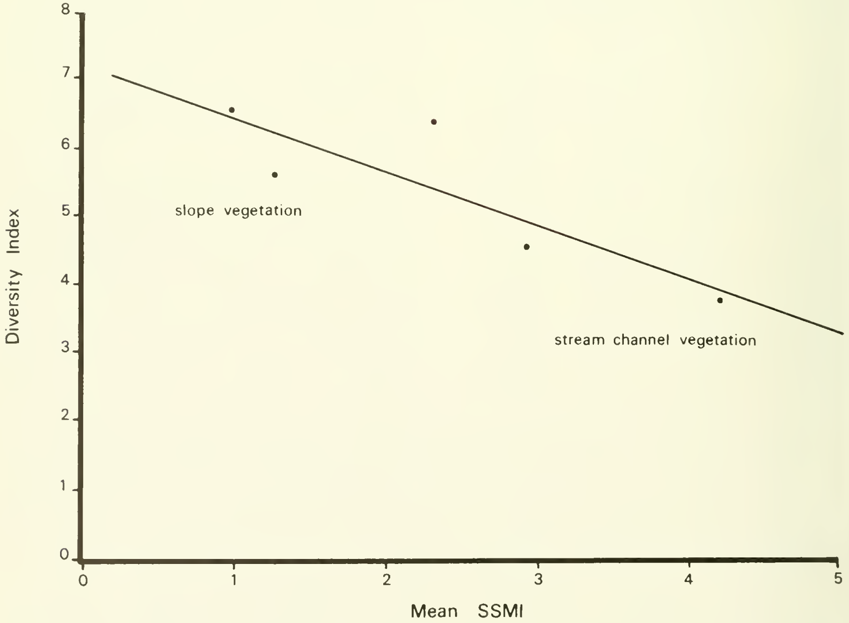

Fig. 11. Regression analysis of relationship between DI and SSMI.

terpreted if other environmental parameters (i.e., disturbance, etc.) had been measured. Regression analysis of DI vs. SSMI exhibited a negative correlation at .001 level of significance and had an $r^2$ value of .74.

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# ECOLOGICAL AND COMMUNITY RELATIONSHIPS OF *ERIOGONUM CORYMBOSUM* (POLYGONACEAE) IN THE UINTA BASIN, UTAH

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Abstract.— Ecological and community relationships of 10 different plant communities in the Uinta Basin, Utah, where *Eriogonum corymbosum* was found to grow were studied and described. Each community was sampled to determine the amount of ground cover, percent composition, frequency, and density of participating species. Physical site factors, viz., soil texture, total soluble salts, pH, cation exchange capacity, and amounts of calcium, magnesium, potassium, and sodium were determined. The 10 communities were compared to determine the degree of similarity between them. Correlations between individual plant species and measurable characteristics of the community were attempted. Evidence is presented that the distributional patterns of some species are related to these measured characteristics. *Eriogonum corymbosum, Chenopodium leptophyllum, Atriplex confertifolia, Stipa comata, Artemisia tridentata,* and *Agropyron smithii* showed correlation to both vegetational and edaphic factors of the community.

Total vegetative cover increased from desert to mountain in the Uinta Basin. As the vegetative cover increased, soil depth also increased. *Eriogonum corymbosum* decreased in importance in the higher elevation communities.

*Eriogonum corymbosum* was studied taxonomically, which demonstrated the presence of a previously undescribed variety. It is suggested that *E. corymbosum* var. *corymbosum,* found generally in the desert areas of the basin, is composed of a series of ecotypes that inhabit shallow soils and prefer communities that show high degrees of disturbance, little competition, fairly high levels of soluble salts in the soil, and are found at elevations below 5500 feet. *Eriogonum corymbosum* var. *erectum,* on the other hand, does best in communities above 6000 feet that show less disturbance than the desert areas, have deeper soils, and low levels of soluble salts.

*Eriogonum corymbosum* Benth. in DC (wild buckwheat) is a low-growing, perennial shrub that occurs in much of the cold temperate desert shrub regions of Colorado, Utah, and Nevada. In the Uinta Basin its growth is widespread on several different geological formations. In some areas its distribution is restricted to a specific formation, while elsewhere its distribution appears unrestricted.

The ecology of *E. corymbosum* is not well known, and available literature on the subject is fragmentary and scattered. Welsh (1957), in a study of the Dinosaur National Monument in the Uinta Basin, Utah, describes its occurrence on the Moenkopi and Mowry shale formations. He states that it appears to be restricted to these formations and grows only where the formations are fully exposed. It is the dominant plant of much of the Mowry Shale formation.

In an ecological study of the Flaming Gorge Reservoir Basin, Flowers (1957) lists *E. corymbosum* as a member of a zone of vegetation forming a junction between the river banks and the uplands, where it appears frequently on dry hillsides at about 1700 m (5600 feet). Graham (1937) found it growing with sagebrush on Red Creek.

Many writers have noted that plants are indicators of certain soils and geological formations. Graham (1937) wrote of the existence of endemics on the Green River shale formation in the Uinta Basin. Cannon (1952) noted the correlation between uranium-vanadium deposits and vegetation. Mason (1946) states that some soils, such as the serpentine soils, are well known for the endemic species that occur on them. Krucheberg (1951, 1954), Whittaker (1954), and Waler (1954) note a correlation between endemics and indicator species of the serpentine soils of California.

Kearney et al. (1914) in Tooele Valley, Utah, found that different types of native vegetation indicated conditions of moisture and salinity of the soil on which they were found. Shantz and Piemeisel (1940) found conditions in Escalante Valley, Utah, similar to those found in Tooele Valley, Utah, by Kearney et al. (1914). Fautin (1946) noted shadscale scattered in the more xeric and higher saline areas of valleys in central Utah. Billings (1949, 1950, 1951, 1952) states that chemical differences in soils may produce marked differences in the vegetation within fairly uniform climatic areas, that vegetation zones can be correlated with climatic and soils factors, and that the mosaic of smaller vegetational differences within a large zone may be caused by edaphic factors. He also noted *Atriplex confertifolia* to be an indicator of subsoil salinity. Gates et al. (1956) considered the edaphic factors, soluble salts, saturated extract conductivity, and exchangable sodium, to be of primary importance in determining the distribution of some shrub types. Thatcher (1959) and Robertson et al. (1966) found that *Artemisia tridentata* occurred only on moderately deep to deep, loamy soils.

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Little has been published on the subject of indicator species concerned with the cold temperate desert shrub regions of the west. A knowledge of indicator species such as *E. corymbosum* is desirable because this species grows on peculiar soil types (i.e., soils of high or low pH, high or low salt content, etc.) and thus becomes important to the ecologist attempting to delineate or describe areas of the cold temperate regions.

During this study, I recognized from an ecological standpoint two distinct varieties. Consequently, the two varieties were named *E. corymbosum* Benth. in DC var. *corymbosum* and *E. corymbosum* Benth. in DC var. *erectum* Reveal and Brotherson (Reveal 1967).

*Eriogonum corymbosum* var. *corymbosum* has its distribution centered mainly in northeastern and central Utah, but it extends into northwestern Colorado and extreme southwestern Wyoming. It also extends southward to northcentral and northwestern Arizona.

*Eriogonum corymbosum* var. *erectum* is widely scattered in northeastern Utah, extending from western Wasatch County to extreme western Uintah County, mainly above 1800 m (6000 feet) elevation.

## Study Area

The Uinta Basin is a broad, elongated, asymmetric basin lying in the northeastern corner of Utah and extending into northwestern Colorado. It is both a structural and a topographic basin and is a subdivision of the Colorado Plateau province (Marsell 1964). It encompasses some 12,000 square miles and is about 150 miles (240 km) long in an east-west direction and 100 miles (160 km) wide in a north-south direction (Dastrup 1963).

The basin's northern boundary (Fig. 1) is in the Uinta Mountains, which reach elevations of 4100 m (13,500 feet). On the south it is bounded by the rim of the Tavaputs Plateau, which appears to rise roughly but steadily to a dip slope. Its west rim is flanked by the eastern slopes of the Wasatch Mountains, but its eastern side is not so sharply defined topographically (Marsell 1964).

Much of the central portion of the Uinta Basin is desert with an annual precipitation of less than 24 cm (10 inches). The gently sloping floor lies between 1500 m (5000 feet) and 1800 m (6000 feet) in elevation, but it reaches as much as 2100 m (7000 feet) at the foot of the Uinta Mountains.

The basin is drained in a somewhat centripetal pattern by three major streams and their tributaries (Fig. 1). The Duchesne River flows in a southeast direction and the White River flows westward. These two streams, along with their tributaries, drain the entire basin excepting the northeast corner. This corner is drained by the third major stream, the Green River, which crosses the East Tavaputs Plateau to meet the Colorado. The Duchesne and its tributaries (Rock Creek, Yellowstone River, Lake Fork, and the Uinta River) drain almost the entire Utah part of the basin, and the White River drains the Colorado portion. The Strawberry River, found in the western end, is the only stream of any size that drains the southern part of the basin (Marsell 1964, Dastrup 1963).

The land surface of the basin is rough and broken, cut in many places by deep gorges. Bare rock surfaces are widely scattered, forming cliffs, deep slopes, and stripped surfaces in many places. The soil is highly variable, ranging from deep, heavy clays to shallow, sandy soils. In much of the basin a calcareous layer can be found (Marsell 1964).

## Geology

The Uinta Basin is a typical Rocky Mountain-type assymetric Tertiary basin. It was formed by the gradual settling of the interior area below the surface of deposition and concurrent lesser sinking or upward movement of the basin rims. Its development began in the Paleocene or Eocene and has continued until the present. As before stated, the basin is both a topographic and a structural basin. It exhibits from 900 m (3000 feet) to 1800 m (6000 feet) of relief between its lowest basin parts and the highest rim. The basin represents a superficial expression of the Tertiary structural basin and would still be filling with sediment except for the Green River, which has breached the north and south rims (Osmond 1964).

The basin contains a large number of geological formations, each having its own age and period of development. Seven of these formations furnish substrata for the 10 different communities analyzed in this study. These 7 formations (in sequence from the oldest to the youngest) are: Ankareh, Moenkopi, Mowry Shale, Parachute Creek and Evacuation Creek (members of the Green River formation), Uinta, Duchesne River, and glacial moraines.

## Methods

Ten study areas were established throughout the Uinta Basin (Fig. 1). The areas were chosen on the basis that *Eriogonum corymbosum* was present in the vegetational cover and by the geological formations upon which they occurred. Vegetational data and soil samples were collected during the summer

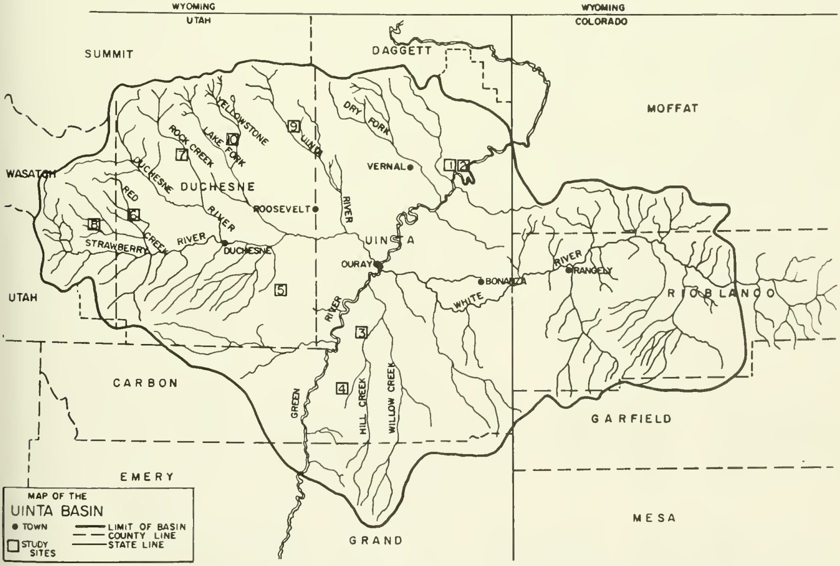
WYOMING
UTAH
WYOMING
COLORADO
SUMMIT
DAGGETT
MOFFAT
WASATCH
DRY FORK
YELLOWSTONE
LAKE FORK
ROCK CREEK
UINTA
VERNAL
DUCHESNE
DUCHESNE
RED
RIVER
ROOSEVELT
RIVER
STRAWBERRY
CREEK
RIVER
DUCHESNE
UINTA
OURAY
BONANZA
RIVER
RANGELY
WHITE
RIO BLANCO
UTAH
RIVER
GREEN
HILL CREEK
WILLOW CREEK
CARBON
GARFIELD
EMERY
MESA
GRAND
1
2
3
4
5
6
7
8
9
10
MAP OF THE
UINTA BASIN
TOWN
STUDY SITES
LIMIT OF BASIN
COUNTY LINE
STATE LINE

Fig. 1. Map of the Uinta Basin showing study site locations.

months (June through August) and analyzed in the laboratory during winter.

Vegetation data were gathered in midsummer (July 15 to August 10) when *E. corymbosum* and most other species had reached their maximum growth. Collecting of voucher specimens was done throughout the growing season. All specimens were deposited in the Brigham Young University herbarium.

The vegetational cover of each area was analyzed by employing the line-point method (Cain and Castro 1959). Ten 15-m (50-feet) transects were taken in each area, with the points distributed every 7 cm (3 inches) along the transect. This gave a total of 200 points per transect or 2000 points per area. Transects were located on a restricted random basis to eliminate bias and keep adjacent transects equal distances apart. At each point along the transect a seven-gage sharpened wire was lowered toward the ground and records were made of the first and all successive species hits. Where no vegetation occurred for the wire to touch, the hits were recorded as litter, rock, or bare ground.

Frequency and density data were acquired by use of a meter square quadrat placed at 3-m (10-foot) intervals along the 15-m transects. This gave a total of 50 quadrats per area. Frequency and density data were recorded only for shrubs, trees, and bunch grasses.

Percent surface cover for individual species and percent total vegetation cover were calculated as follows:

$$\text{\% surface cover for each species} = \frac{\text{Total hits for each species}}{\text{Total points}} \times 100$$

$$\text{\% total vegetational cover} = \frac{\text{Total hits for all species minus overlapping hits}}{\text{Total points}} \times 100$$

$$\text{\% composition of each species} = \frac{\text{Total hits for each species}}{\text{Total hits for all species}} \times 100$$

Percent frequency figures and density figures were obtained through use of the following relationships:

$$\text{\% frequency} = \frac{\text{Total quadrats a species appears in}}{\text{Total quadrats}} \times 100$$

Density = # plants/50 quadrats × 83.00 50 quadrats /acre[2]

Differences and similarities between the different study sites were computed utilizing Sorensen's index of similarity (Sorensen 1948), as adapted by Dix and Butler (1960). The formula was as follows:

$$K = 2W/a + b \times 100.$$

K is the similarity index between two sites; a represents the sum of the coverage percentages of all species in one stand; b represents a similar figure for a second stand. W represents that part of the cover common to the species found in both stands. After the indices were obtained, an ordination matrix was constructed (Table 4). This placed the most similar sites next to each other and the more dissimilar sites at opposite ends of the matrix. The sites were then divided into four groups and a table (Table 6) was constructed from

TABLE 1. Site characteristics associated with 10 study areas.

| Site | Soil depth (dm) | % Exposed bare ground | % Exposed rock | % Litter cover |
|---|---|---|---|---|
| Mowry | 1.86 | 57.80 | 0.00 | 2.15 |
| Moenkopi | 4.36 | 76.50 | 2.00 | 0.10 |
| Evacuation Creek | .98 | 59.00 | 9.40 | 4.10 |
| Parachute Creek | 1.77 | 56.50 | 6.25 | 2.75 |
| Wells Draw | 1.21 | 62.80 | 2.00 | 2.15 |
| Red Creek | 5.06 | 45.30 | 13.50 | 6.00 |
| Rock Creek | 3.32 | 13.80 | 7.80 | 6.60 |
| Strawberry Valley | 2.81 | 29.25 | 2.25 | 4.10 |
| Uinta River | 4.96 | 9.55 | 0.15 | 5.70 |
| Yellowstone River | 7.31 | .90 | 0.00 | 4.25 |

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[2] This number (83.00 50 quadrats/acre) was obtained by dividing the number of square feet in 50 quadrats (i.e., 524.800 square feet/50 quadrats) into the number of square feet in an acre (i.e., 43,560 square feet/acre).

TABLE 2. Soil data for each study site by horizon. Each figure represents an average for three pits at each site.

| Depth (in inches) | Sand % | Silt % | Clay % | pH 1:1 | Soluble salts (ppm) | CEC in Meq./ /100 g. | Ca % | Mg % | K % | Na % |
|---|---|---|---|---|---|---|---|---|---|---|
| Mowry Formation | | | | | | | | | | |
| Surf. | 65 | 17 | 18 | 6.4 | 1099 | 36.88 | 53.4 | 28.3 | 9.7 | 8.1 |
| 0–6 | 63 | 18 | 18 | 4.8 | 1295 | 46.59 | 57.0 | 28.6 | 6.4 | 8.0 |
| 6–12 | 64 | 13 | 14 | 3.8 | 1127 | 48.61 | 61.8 | 23.4 | 5.7 | 9.0 |
| 12–18 | 63 | 13 | 15 | 3.7 | 1023 | 44.66 | 62.8 | 22.3 | 5.7 | 9.5 |
| Moenkopi Formation | | | | | | | | | | |
| Surf. | 41 | – | – | 7.9 | 818 | 8.57 | 80.4 | 7.4 | 2.8 | 9.5 |
| 0–6 | 54 | – | – | 8.0 | 887 | 8.83 | 79.8 | 7.0 | 4.1 | 9.0 |
| 6–12 | 62 | – | – | 7.9 | 1214 | 9.29 | 72.1 | 9.2 | 6.1 | 9.9 |
| 12–24 | 65 | – | – | 7.9 | 1440 | 9.54 | 70.0 | 10.3 | 7.2 | 10.5 |
| 24–36 | 61 | – | – | 8.1 | 1875 | 8.84 | 68.2 | 13.0 | 7.5 | 10.8 |
| Evacuation Creek Member | | | | | | | | | | |
| Surf. | 83 | 10 | 7 | 8.5 | 208 | 11.39 | 69.4 | 12.1 | 4.2 | 14.4 |
| 0–6 | 72 | 18 | 10 | 8.7 | 256 | 16.20 | 70.8 | 12.5 | 4.1 | 12.6 |
| 6–12 | 74 | 11 | 16 | 8.8 | 267 | 16.35 | 65.5 | 14.3 | 3.3 | 17.0 |
| Parachute Creek Member | | | | | | | | | | |
| Surf. | 71 | 22 | 8 | 8.3 | 530 | 20.33 | 66.7 | 21.1 | 2.8 | 9.1 |
| 0–6 | 58 | 26 | 16 | 8.3 | 550 | 24.03 | 58.6 | 29.7 | 2.3 | 9.1 |
| 6–18 | 68 | 25 | 7 | 8.1 | 630 | 25.38 | 55.6 | 34.4 | 1.9 | 8.3 |
| 18–24 | – | – | – | 8.2 | 373 | – | – | – | – | – |
| Wells Draw | | | | | | | | | | |
| Surf. | 78 | 18 | 3 | 8.4 | 196 | 13.27 | 76.9 | 7.9 | 6.9 | 8.2 |
| 0–6 | 69 | 23 | 8 | 8.5 | 234 | 16.75 | 76.1 | 10.5 | 5.5 | 9.8 |
| 6–12 | 62 | 23 | 10 | 8.2 | 401 | 23.71 | 70.9 | 12.5 | 3.3 | 13.4 |
| 12–24 | 80 | 16 | 4 | 8.5 | 229 | 17.94 | 78.1 | 9.9 | 1.6 | 10.4 |
| Red Creek | | | | | | | | | | |
| Surf. | 42 | 37 | 24 | 8.8 | 386 | 14.88 | 48.4 | 41.2 | 5.1 | 5.4 |
| 0–6 | 32 | 46 | 22 | 9.0 | 410 | 16.75 | 38.1 | 50.9 | 4.3 | 6.8 |
| 6–12 | 27 | 47 | 26 | 9.2 | 461 | 16.62 | 31.8 | 54.5 | 5.2 | 8.5 |
| 12–24 | 32 | 43 | 26 | 9.5 | 519 | 14.75 | 30.3 | 50.5 | 3.7 | 15.5 |
| 24–36 | 44 | 38 | 18 | 9.6 | 630 | 14.08 | 28.1 | 49.8 | 4.3 | 17.8 |
| Rock Creek | | | | | | | | | | |
| Surf. | 53 | 35 | 12 | 8.3 | 271 | 11.69 | 65.2 | 18.5 | 10.3 | 6.0 |
| 0–6 | 55 | 34 | 11 | 8.3 | 261 | 13.36 | 59.6 | 23.5 | 10.4 | 6.5 |
| 6–12 | 54 | 36 | 10 | 8.5 | 248 | 12.31 | 59.0 | 28.2 | 7.0 | 5.4 |
| 12–24 | 48 | 37 | 12 | 8.4 | 274 | 9.96 | 53.7 | 30.3 | 9.5 | 6.5 |
| 24–36 | 45 | – | – | 8.2 | 924 | 5.38 | 61.9 | 31.0 | 7.9 | 7.4 |
| Strawberry Valley | | | | | | | | | | |
| Surf. | 51 | 29 | 20 | 8.2 | 305 | 8.83 | 62.7 | 20.4 | 10.0 | 6.9 |
| 0–6 | 50 | 30 | 20 | 8.3 | 357 | 8.63 | 58.5 | 26.9 | 6.9 | 7.9 |
| 6–12 | 43 | 38 | 19 | 8.5 | 279 | 10.63 | 55.6 | 32.9 | 4.3 | 7.1 |
| 12–24 | 51 | 34 | 15 | 8.7 | 211 | 6.35 | 55.3 | 34.3 | 4.3 | 6.1 |
| Uinta River | | | | | | | | | | |
| Surf. | 59 | 28 | 13 | 7.3 | 308 | 15.88 | 56.3 | 24.1 | 12.7 | 6.9 |
| 0–6 | 58 | 27 | 14 | 7.8 | 391 | 19.36 | 56.6 | 22.3 | 13.7 | 7.4 |
| 6–12 | 58 | 25 | 17 | 8.0 | 400 | 19.45 | 54.8 | 23.8 | 14.3 | 7.1 |
| 12–24 | 60 | 23 | 17 | 8.1 | 394 | 18.07 | 51.9 | 27.1 | 13.9 | 7.0 |
| 24–36 | 60 | 22 | 18 | 8.2 | 410 | 17.43 | 49.6 | 29.4 | 13.9 | 6.7 |
| Yellowstone River | | | | | | | | | | |
| Surf. | 80 | 16 | 5 | 5.9 | 42 | 8.54 | 66.3 | 15.6 | 9.1 | 9.1 |
| 0–6 | 83 | 12 | 4 | 6.7 | 47 | 5.83 | 66.0 | 18.4 | 6.8 | 9.0 |
| 6–12 | 89 | 7 | 4 | 6.7 | 46 | 4.45 | 62.9 | 21.1 | 7.6 | 8.8 |
| 12–24 | 85 | 10 | 4 | 6.8 | 35 | 4.77 | 63.6 | 22.0 | 5.0 | 9.5 |
| 24–36 | 87 | 8 | 4 | 6.8 | 36 | 4.42 | 60.9 | 23.6 | 6.1 | 9.4 |

these by averaging the cover percents for each species within the group. Those plant species showing the highest preference for group 1 were placed at the top of the table, and those species showing the least preference were placed at the bottom. From this table, 15 indicator species were selected and given adaptation numbers. Those species with the greatest preference for Group 1 were given the number one and those with the greatest preferences for Group 4 were assigned the number five.

By use of the selected indicator plants, Plot Index Values (PIV) for the 10 sites were obtained by applying the following formula (Dix and Butler 1960):

$$\text{PIV} = \frac{\text{Sum (relative composition of each indicator species} \times \text{its adaptation \#)}}{\text{Sum (relative composition of each indicator species)}}$$

From the Plot Index Values a linear ordination (Fig. 2) was constructed. Environmental correlations were then attempted with the use of this ordination.

A list was made of all plants noted in each area, and a composition study was made (Table 10) to indicate which families were the best represented in each area. All plant specimens collected during this study were deposited in the herbarium of the Brigham Young University.

Three soil pits were dug at each study area, and soil samples containing a composite sample of several hundred grams were taken from the surface, 0–15, 15–30, 30–60, 60–90 cm depths.

Soil depth was determined for each area by using pits and a 10-dm penetrometer (a sharpened ⅜" steel rod). The penetrometer was pushed into the ground at 10-foot intervals along the 50-foot transects used to collect the vegetational data.

Textural analysis of the soil was determined according to Bouyoucos (1936, 1951). Hydrogen ion concentration was determined for the same group of samples on a saturated paste, a 1:1 and a 1:5 ratio of soil to water. The 1:1 and 1:5 ratios were measured to indicate sodium content. A Beckmann glass electrode pH meter was used and the samples were prepared as outlined by Russell (1948).

Total soluble salts for the above-mentioned saturated pastes were determined by the use of a Wheatstone electrical conductivity bridge.

Cation exchange capacities for all collected soil samples were determined by using the standard ammonium acetate extraction method described by Russell (1948). Analysis for the amount of available calcium, magnesium, potassium, and sodium was found by using the ammonium acetate extraction from the cation exchange capacity determinations and a Beckmann model DU flame photometer.

## Results and Discussion

The 10 study sites were located throughout the Uinta Basin (Fig. 1). General physical and biological factors characteristic of these sites can be seen in Tables 1, 2, 3, and 8. Those sites located in the south and eastern parts of the basin showed shallow soils, little litter cover, and large exposed areas of bare ground. In contrast, those sites located in the western and northern parts of the basin exhibit deeper soils, increased amounts of litter cover, and much less exposed soil surface (Table 1).

Texturally the soils varied from sand to loams to sandy clay loams, with no distinct patterns being evident (Table 2). Soluble salt concentrations and cation exchange capacities generally increased from the north and

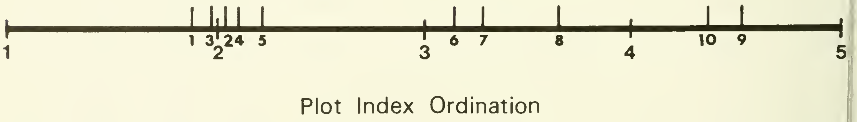

Fig. 2. The plot index values ordination. The linear arrangement of the 10 study sites according to their plot index values.

west parts of the basin toward the south and east parts. Hydrogen ion concentration (pH) varied from lows of 3.7 on the Mowry Shale formation to 9.6 in Red Creek on the Uinta formation, but again showed no distinct geographical patterns. Calcium and magnesium were the most abundant of the cations measured, with potassium and sodium seldom comprising over 10 to 20 percent of cation exchange capacity (Table 2).

Vegetationally the sites located in the north and west parts of the basin showed the highest shrub densities, even though grasses were the dominant life form type with regard to cover. Shrub cover, on the other hand, was the most important in the south and east parts of the basin (Table 3). Forb and annual plant cover showed no observable patterns. Total cover and diversity patterns (Table 3), in contrast to bare ground (Table 1), were highest near the mountains in the north and west basin areas. Numbers of species per study site varied from 11 to 29, with an average of 22. The prevalent species (the 24 most prominent species found to occur across the study area) are listed in Table 8. It can be seen they represent a rather typical assemblage of the cold temperate desert shrub areas of the intermountain region.

TABLE 5. Study site groups as determined from the similar index matrix.

| Group | Study site |
|---|---|
| 1 | Mowry study site<br>Parachute Creek member of the Green River Formation study site |
| 2 | Evacuation Creek member of the Green River Formation study site<br>Moenkopi study site |
| 3 | Red Creek study site<br>Rock Creek study site |
| 4 | Strawberry Valley study site<br>Uinta River study site<br>Yellowstone River study site |

TABLE 3. Vegetation characteristics associated with the 10 study sites.

| Site | Total cover | Percent cover | | | | Shrub density (plants/Acre) | Diversity* |
|---|---|---|---|---|---|---|---|
| | | Shrub | Forb | Grass | Annual | | |
| Mowry | 40.1 | 78.0 | 17.0 | 4.0 | 1.0 | 7300 | .17 |
| Moenkopi | 20.5 | 81.0 | 15.0 | 3.0 | 1.0 | 2515 | .24 |
| Evacuation Creek | 27.5 | 77.0 | 4.0 | 7.0 | 12.0 | 8449 | .41 |
| Parachute Creek | 34.5 | 64.0 | 1.0 | 32.0 | 3.0 | 4542 | .34 |
| Wells Draw | 33.5 | 68.0 | 1.0 | 20.0 | 11.0 | 7138 | .40 |
| Red Creek | 34.8 | 68.0 | 0.5 | 30.0 | 2.0 | 15572 | .53 |
| Rock Creek | 72.6 | 28.0 | 3.0 | 65.0 | 4.0 | 15660 | .44 |
| Strawberry Valley | 64.4 | 39.0 | 13.0 | 45.0 | 3.0 | 24652 | .82 |
| Uintah River | 84.6 | 37.0 | 9.0 | 51.0 | 4.0 | 37716 | .69 |
| Yellowstone River | 94.9 | 22.0 | 4.0 | 60.0 | 14.0 | 7301 | .53 |

*Diversity = $1/\Sigma pi^2$

TABLE 4. Similarity index matrix for the 10 study sites: Mowry = 1; Moenkopi = 2; Evacuation Creek = 3; Parachute Creek = 4; Wells Draw = 5; Red Creek = 6; Rock Creek = 7; Strawberry = 8; Uinta = 9; Yellowstone = 10.

| | 1 | 4 | 3 | 2 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | — | 48.0 | 45.6 | 45.0 | 40.6 | 32.1 | 20.8 | 17.1 | 17.5 | 11.7 |
| 4 | | | 57.6 | 50.5 | 46.0 | 35.2 | 25.3 | 21.2 | 17.3 | 14.7 |
| 3 | | | | 62.4 | 45.7 | 35.5 | 22.5 | 18.9 | 17.8 | 12.9 |
| 2 | | | | | 50.2 | 39.1 | 23.1 | 17.6 | 15.7 | 11.6 |
| 5 | | | | | | 31.7 | 29.8 | 25.6 | 18.3 | 13.2 |
| 6 | | | | | | | 50.6 | 21.6 | 16.2 | 17.5 |
| 7 | | | | | | | | 24.2 | 27.8 | 29.3 |
| 8 | | | | | | | | | 25.5 | 33.5 |
| 9 | | | | | | | | | | 62.2 |
| 10 | | | | | | | | | | — |

## Ordination Analysis

Analysis of the vegetation of the different areas and of the areas themselves was attempted by evaluating the differences and similarities between sites. To accomplish this, the areas were ordered by application of an index of similarity (Table 4).

The matrix was designed to place those sites with the greatest similarities closest together and those with the greatest differences farthest apart. Therefore, the Moenkopi and the Evacuation Creek sites are interpreted to be the most similar and will thus exhibit similar community characteristics, and the Moenkopi and the Yellowstone sites are the most dissimilar and should exhibit few factors in common. The position of each area within the matrix was determined by placing the highest index values along the diagonal of the square and the lowest index values toward the upper right-hand corner of the table. The magnitude of the indices decreases from left to right when comparing the Mowry study site with the Yellowstone River study site or the other sites listed to the right of the Mowry. Similarly, the indices increase from top to bottom or from right to left when the other areas are compared to the Yellowstone River study site.

TABLE 6. Average percent composition values in the four groups for all species with a percent composition greater than 0.50 percent.

| | Plant species | Groups | | | |
|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 |
| *1 | Atriplex confertifolia | 5.68 | 4.37 | | |
| 1 | Chenopodiuum leptophyllum | 4.98 | 2.90 | 0.43 | 0.07 |
| 1 | Gila leptomeria | 3.42 | 1.10 | | 1.66 |
| 2 | Ephedra torreyana | | 3.07 | | |
| | Astragalus saurinus | | 2.20 | | |
| | Juniperus utahensis | 2.01 | | 2.68 | |
| | Stanleya pinnata | | 1.73 | | |
| 2 | Eriogonum corymbosum | 61.05 | 48.78 | 34.40 | 8.51 |
| 2 | Tetradymia spinosa | | 4.96 | | |
| | Mentzelia dispersa | 0.25 | 0.68 | | |
| 3 | Amelanchier utahensis | | 1.28 | 1.10 | 0.25 |
| | Poa secunda | 1.28 | | 0.38 | 1.40 |
| | Chrysothamnus parryi | | 0.37 | | 0.86 |
| 3 | Oryzopsis hymenoides | 3.91 | 7.01 | 4.94 | 7.98 |
| 3 | Agropyron trachycaulum | | 0.24 | 33.10 | 0.16 |
| 4 | Chrysothamnus viscidiflorus | 0.27 | 1.50 | 1.03 | 5.70 |
| | Artemisia nova | | 9.60 | | |
| | Lepidium montanum | | 1.31 | | |
| | Solidago petradoria | | 0.87 | | |
| | Poa palustris | | | | 1.2 |
| | Tetradymia glabrata | | | | 1.3 |
| | Astragalus tenellus | | | | 3.1 |
| 4 | Cercocarpus montanus | | | 14.16 | |
| | Sitanion hystrix | 0.12 | 0.18 | 0.16 | 0.3 |
| 4 | Artemisia tridentata | 1.78 | | 6.35 | 8.31 |
| | Purshia tridentata | | | | 0.2 |
| | Astragalus convallarius | | | | 1.0 |
| | Sphaeralcea coccinea | | | 0.48 | 1.4 |
| | Lappula redowskii | | 0.97 | 0.46 | 0.31 |
| | Chrysothamnus nauseosus | | | | 1.3 |
| | Opuntia polyacantha | | | 0.08 | 1.3 |
| | Lepidium densiflorum | | | | 1.0 |
| 5 | Xanthocephalum sarothrae | | | | 4.2 |
| 5 | Agropyron smithii | | | | 20.6 |
| 5 | Stipa comata | 018 | | 6.65 | 26.1 |

*These numbers are adaptation numbers and were assigned to different indicator species. The indicator species were chosen on the basis of their indicated preference for a certain group or groups as shown in the above table.

To help understand the association of individual species to these relationships, the areas listed on Table 4 were divided into the four groups shown in Table 5.

The percent composition figures of all species with percents greater than 0.50 percent were then averaged in each group. A list (Table 6) was then prepared placing those species with the greatest preference for Group 1 at the top and those species with the greatest preference for Group 4 at the bottom of the list. You can now determine some characteristic distribution or associational patterns for many of the individual species.

TABLE 7. Plot index values (PIV) for 10 study sites.

| | Study Site | PIV |
|---|---|---|
| 1 | Mowry | 1.86 |
| 4 | Parachute Creek | 2.08 |
| 3 | Evacuation Creek | 1.95 |
| 2 | Moenkopi | 2.03 |
| 5 | Wells Draw | 2.21 |
| 6 | Red Creek | 3.14 |
| 7 | Rock Creek | 3.28 |
| 8 | Strawberry Valley | 3.65 |
| 9 | Uinta River | 4.51 |
| 10 | Yellowstone River | 4.37 |

Although Table 4 served effectively to segregate the different study areas, it did not show the degree of compositional differences or similarities actually existent between them. Because such information was desirable, Plot Index Values (PIV) (Table 7) described by Dix and Butler (1960) were employed to assign a spatial position to each study site on a linear ordination and thus to actually measure to some degree the ecological distance between the different areas of study. To accomplish this, 15 indicator species were chosen from the list in Table 6 and assigned adaptation numbers from 1 to 5. Those species with the greatest preference for Group 1 were assigned the adaptation number 1, and those with the least preference for Group 1 were assigned adaptation number 5. Under such a system, an area will have a PIV of 1 when it contains only indicator species assigned adaptation numbers of 1. Likewise, an area will have a PIV of 5 when it contains only indicator species as-

TABLE 8. Prevalent species list for 10 study sites along with average percent cover in the different areas sampled.

| Species | Importance value | Study site | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1* | 3 | 2 | 4 | 5 | 6 | 7 | 8 | 10 | 9 |
| Eriogonum corymbosum | 1421.5 | 30.8 | 13.2 | 13.6 | 17.7 | 13.9 | 11.5 | 11.9 | 9.1 | 13.3 | 7.4 |
| Stipa comata | 563.1 | .2 | | | | .4 | | 12.5 | 1.5 | 50.9 | 28.6 |
| Oryzopsis hymenoides | 389.5 | .3 | .7 | .4 | 2.7 | 6.4 | 1.2 | 6.9 | 18.8 | 1.2 | 2.4 |
| Agropyron smithii | 380.8 | | | | | | | | 14.7 | 38.0 | 23.3 |
| Artemisia tridentata | 285.9 | | | | 1.3 | .2 | 3.5 | 4.4 | 3.2 | 14.3 | 13.9 |
| Agropyron trachycaulum | 202.8 | | | .2 | | | 10.4 | 39.5 | | | .6 |
| Xanthocephalum sarothrae | 113.3 | | | | | | | | .9 | | 13.3 |
| Bromus tectorum | 106.0 | .4 | | | | .1 | | 2.6 | | 9.4 | .5 |
| Gilia leptomeria | 55.8 | 2.8 | | | | 1.3 | | | .7 | 6.5 | |
| Sphaeralcea coccinea | 42.7 | | | | | | | .9 | | .4 | 4.9 |
| Atriplex confertifolia | 39.3 | | 2.1 | .9 | 4.3 | .6 | | | | | |
| Chenopodium leptophyllum | 37.0 | 3.2 | 2.4 | | .9 | .2 | .2 | .5 | .2 | | |
| Chrysothamnus viscidiflorus | 33.2 | | 1.3 | | .2 | .2 | .6 | .7 | 14.0 | | 1.2 |
| Cercocarpos montanus | 32.7 | | | | | | 9.6 | 6.8 | | | |
| Astragalus tenellus | 25.7 | | | | | | | | 8.6 | | |
| Amelanchier utahensis | 23.1 | | | .8 | | | .6 | .9 | | .2 | .9 |
| Lepidium densiflorum | 22.7 | | | | | | | | | 4.1 | 3.5 |
| Agrophron spicatum | 21.8 | | 1.2 | 4.1 | 8.9 | | | | .8 | | |
| Chrysothamnus nauseosus | 21.6 | | | | | | | | | 2.3 | 2.9 |
| Chenopodium fremontii | 21.6 | | | | | | | | | 3.6 | |
| Artemisia nova | 21.1 | | | | | 10.9 | | | | | |
| Lappula redowskii | 19.8 | | | | | 1.1 | .1 | .7 | | 1.5 | |
| Sitanion hystrix | 18.8 | .1 | .1 | | | .2 | | .3 | | 1.7 | |
| Poa sandbergii | 18.8 | 1.1 | | | | | | .7 | 1.1 | | 3.5 |
| Opuntia polyacantha | 18.0 | | | | | | .6 | .2 | | 3.0 | 2.9 |

*Numbers equivalent to study sites as listed in Table 7.

signed adaptation numbers of 5. Areas which contain a mixture of species having different adaptation numbers will have PIV's intermediate between 1 and 5.

The ordination (Fig. 2) was prepared by placing the computed PIV's so that each area exhibited a linear relationship to all the others.

This ordination (Fig. 2) separates the 10 study sites into two fairly distinct groups. These two groups correlate well with the distributional patterns of the two varieties of *Eriogonum corymbosum* discussed earlier. Variety *corymbosum* occurs in the group to the left, which contains the Mowry Shale study site, the Moenkopi formation study site, the Evacuation Creek and Parachute Creek members of the Green River formation study sites, and the Wells Draw study site. Variety *erectum* occurs in the group to the right, which contains the Rock Creek study site, the Uinta River study site, the Yellowstone River study site, the Strawberry Valley study site, and the Red Creek study site. By consulting Table 4 and Figure 2, we see that those study sites in the eastern and southern part of the basin are much more alike and become less so as you travel west and northward across the basin. Similarly, those study sites in the north and western part of the basin exhibit high indexes of similarity, but as you travel south and eastward across the basin, the sites become less and less alike. Those sites in the eastern and southern parts of the basin occupy areas which belong to the deserts of the Uinta Basin and are below 5500 feet elevation. Those sites in the north and western part of the basin are all above 6000 feet and are either in or very near the Uinta Mountains. This factor would tend to place these sites in areas of higher rainfall, and thus in the nondesert areas of the basin.

The response of the prevalent plant species to the ordination is shown in Table 8. Since the patterns of these species along the ordination do not, in themselves, suggest reasons for or factors involved in their distributional patterns, other ecological data collected during this study were also plotted against the above-described ordination (Figs. 3, 4, 5). This was to determine if any correlation between these factors and distributional patterns might be discovered.

Total cover and soil depth show positive correlation to the ordination; bare ground, cation exchange capacity, and soluble salts are negatively correlated to the ordination and thus may so influence the distributional patterns of those species which showed some correlation with the ordination. The species are *Eriogonum corymbosum*, *Chenopodium leptophyllum*, *Ariplex confertifolia*, *Agropyron smithii*, *Artemisia tridentata*, *Stipa comata*, *Tetradymia spinosa*, *Agropyron trachycaulum*, *Agropyron spicatum*, *Cercocarpus montanus*, and *Xanthocephalum sarothrae*. As is evident from studying Table 8, the above species show definite patterns of distribution along the ordination and these patterns appear restricted to certain areas of the ordination. These species, then, can to some extent be classed as indicators of the areas to which they appear restricted.

The species *E. corymbosum*, *C. leptophyllum*, and *A. confertifolia* show decreasing composition percents from left to right (Table 8), but the composition of *A. smithii*, *A. tridentata*, and *S. comata* increase from left to right (Table 8). Looking at Figures 3 and 4, we see that shrub cover, bare ground, cation exchange capacity, and total soluble salts decrease from left to right, but total cover, grass cover, diversity, and soil depth increase. This would indicate generally that *E. corymbosum*, *C. leptophyllum*, and *A. confertifolia* are best adapted to areas having low diversity, shallow soil, elevated levels of exchangable ions and soluble salts, and little total ground cover. *A. smithii*, *A. tridentata*, and *S. comata*, on the other hand, grow best in areas of high diversity where the soils are moderately deep and low in exchangeable ions and soluble salts and exhibit high degrees of total ground cover.

It is evident that there exist definite relationships between these ecological factors and the distributional patterns of the listed species. From Table 2 and Figures 3, 4, and 5, we see that where total soluble salts and cation exchange capacities are at their peaks and soil depth and total cover are at their lower levels, the plants *E. corymbosum*, *C. leptophyllum*, and *A. confertifolia* reach their greatest importance in the community. In the case of *A. confertifolia*, it occurs only in sites which have appreciable amounts of soluble

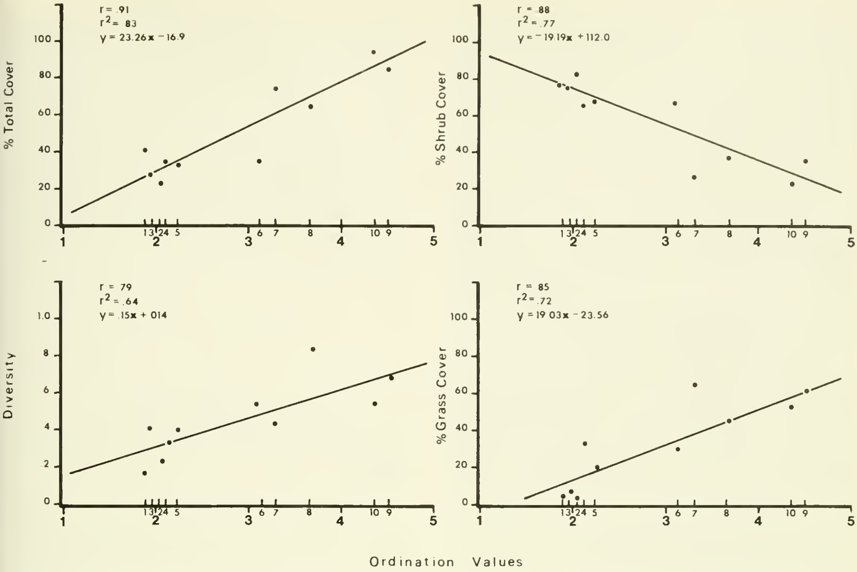

Fig. 3. The relationships of community characteristics (i.e., total cover, diversity, shrub cover, and grass cover) to the ordination. Correlation data are shown.

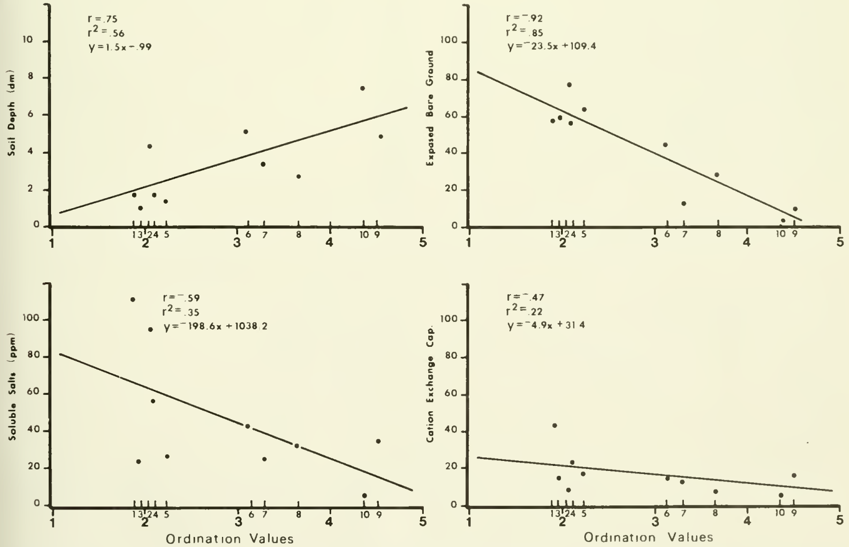

Fig. 4. The relationships of site characteristics (i.e., soil depth, soluble salts, exposed bare ground, and cation exchange capacity) to the ordination. Correlation data are shown.

salts in the soil. Upon examination of the patterns shown by *A. tridentata, A. smithii,* and *S. comata,* we see that they reach their greatest importance where the reverse of the above conditions are true. Indications are that these last three species are able to withstand the competition of other plants more readily than the previous three species.

On further examination of Table 8, another interesting relationship is made apparent. The three species of *Agropyron, A. smithii, A. spicatum,* and *A. trachycaulum* show definite areas of preference or distribution. In each case, the distribution patterns are discrete and show little or no overlap.

Of the other factors examined (i.e., percent sand, silt, clay, pH, and calcium, magnesium, potassium, and sodium), none appeared to have any relationship to the distributional patterns of the species studied. But in some cases, a few of the factors did show distinct relationships to other related soil factors. As the percent sand in the soil decreases, the percent of silt increases. The percent clay appears to show some relationship to the above two factors in that it tends to act somewhat like the silt in relationship to the sand. Calcium and magnesium also show direct correlation (Table 2). As the concentrations of calcium decrease or increase, there is a corresponding increase or decrease in the concentrations of magnesium. The concentrations of potassium and sodium also appeared to be related (Table 2) in that where the levels of sodium are high, the levels of potassium are low and vice versa.

## Family Composition

A total of 173 species of vascular plants, representing a total of 93 genera and 40 families, were collected from the above described study areas. Of these species, 72.7 percent belonged to the families shown in Table 9.

The figures indicate that these nine families contribute about 70 percent of the species to the cold temperate desert shrub re-

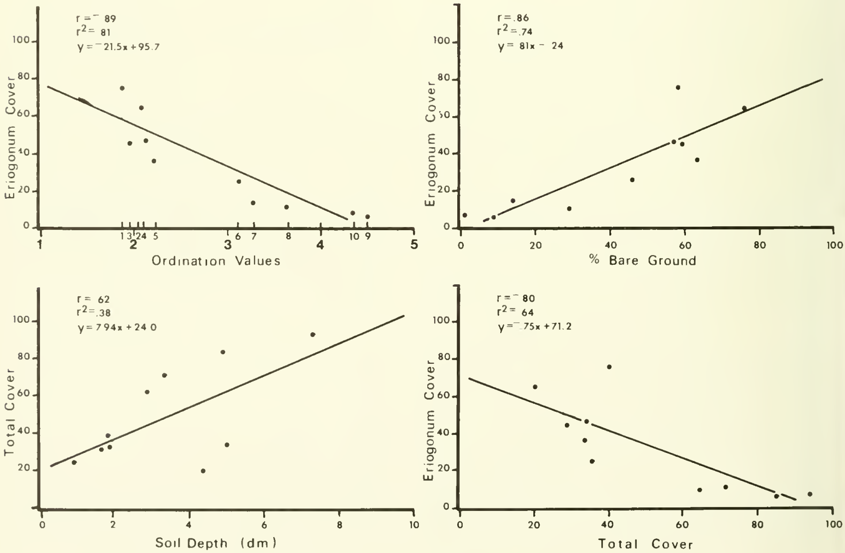

Fig. 5. The relations of *Eriogonum* cover to the ordination and to other site characteristics. Correlation data are shown.

gions of the Uinta Basin, regardless of topography, soil depth, soil texture, soil pH, or other factors measured in this study. A similar family composition chart (Table 10) has been computed on an individual study site basis.

As can be seen, the nine plant families, with the exceptions of Polygonaceae and Chenopodiaceae, and then these only in two of the study areas, show a fair similarity to the earlier figures. The ecological or phytogeographical significance of the dominance of these nine families is not known, but further investigation along such lines tends to hold interest.

## Discussion

There appears in this study evidence that the distributional patterns of some species native to the Uinta Basin are related to measurable characteristics of their communities. *Eriogonum corymbosum, Chenopodium leptophyllum, Atriplex confertifolia, Stipa comata, Artemisia tridentata,* and *Agropyron smithii* are affected by both vegetational and edaphic factors of the community. Being aware that organisms can and do modify the physical environment (Goiger 1957, McIntosh 1957, Polunin 1960), it is still apparent that factors which restrict one species in one community may very well allow other species to reach their greatest importance in another environment.

TABLE 9. Dominant plant family composition of 10 study sites.

| Family | Percent |
|---|---|
| Asteraceae | 22.0 |
| Poaceae | 9.3 |
| Brassicaceae | 8.7 |
| Fabaceae | 5.8 |
| Chenopodiaceae | 5.8 |
| Scrophulariaceae | 5.7 |
| Boraginaceae | 5.7 |
| Polygonaceae | 5.7 |
| Polemoniaceae | 4.0 |
| Total | 72.7 |

The vegetation of the different areas studied showed remarkable similarity at the family level and extreme variability at the species level. There was a definite increase in total vegetative cover, grass cover, and diversity as you moved from southeast to northwest across the Uinta Basin. As the vegetative cover increased, the soil depth also generally increased.

Paralleling these trends, the importance of such plants as *Eriogonum corymbosum, Chenopodium leptophyllum,* and *Atriplex confertifolia* in the community decreased, while such plants as *Stipa comata, Agropyron smithii,* and *Artemisia tridentata* became more important. Other species (i.e., *Gilia leptomeria, Oryzopsis hymenoides, Chrysothamnus viscidiflorus,* and *Amelanchier utahensis*) did not seem to be affected by such trends. The species (Table 8) *Tetradymia spinose, Agropyron trachycaulum, Cercocarpus montanus, Agropyron spicatum,* and

TABLE 10. Comparisons of the total number of plant families, total number of plant species and the percentage of species contributed to the flora by nine major plant families.

| Study Site | Total number families | Total number species | Percent of species in nine plant families | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1* | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| Mowry | 11 | 29 | 17 | 10 | — | — | 28 | 3 | — | 10 | 3 |
| Parachute Creek | 8 | 19 | 37 | 16 | 5 | — | 5 | — | 5 | 16 | 16 |
| Evacuation Creek | 12 | 26 | 27 | 12 | 4 | — | 19 | — | 4 | 8 | 4 |
| Moenkopi | 19 | 39 | 18 | 13 | 8 | 5 | 8 | — | 8 | 8 | 3 |
| Wells Draw | 18 | 51 | 26 | 12 | 8 | 2 | 12 | 2 | 4 | 6 | 6 |
| Red Creek | 15 | 37 | 27 | 8 | 8 | 8 | 8 | 8 | 3 | 8 | — |
| Rock Creek | 14 | 35 | 23 | 17 | 3 | 6 | 3 | 6 | 3 | 3 | 3 |
| Strawberry Valley | 15 | 45 | 24 | 13 | 2 | 11 | 4 | 13 | 2 | 7 | 4 |
| Uinta River | 16 | 43 | 26 | 12 | 5 | 9 | 5 | 7 | 7 | 5 | 5 |
| Yellowstone River | 16 | 43 | 23 | 12 | 5 | — | 2 | 2 | 7 | 14 | 5 |

*1 = Asteraceae; 2 = Poaceae; 3 = Brassicaceae; 4 = Fabaceae; 5 = Chenopodiaceae; 6 = Scrophulariaceae; 7 = Boraginaceae; 8 = Polygonaceae; 9 = Polemoniaceae.

*Xanthocephalum sarothrae* showed definite correlation to certain study sites, but the basis for such correlation was not determined.

Of the edaphic factors measured, soil depth, soluble salts, and cation exchange capacity showed positive relationships to the distribution patterns of the above-mentioned species. The distributional patterns of *Artemisia tridentata* and *Atriplex confertifolia* were found to be in agreement with Kearney et al. (1914), Fautin (1946), Thatcher (1959), and Robertson et al. (1966). *A. tridentata* occurred near the mountains on soils moderately deep to deep exhibiting fairly low levels of soluble salts. *A. confertifolia* was found only where the soils showed fairly high levels of soluble salts and where the soils were generally shallow. Paralleling *A. tridentata* are the distributional patterns of *Agropyron smithii* and *Stipa comata*. The distribution patterns of *Chenopodium leptophyllum* and *Eriogonum corymbosum* show some relationship to that of *A. confertifolia*.

Factors of the soil, such as pH, concentrations of the cations calcium, magnesium, potassium, and sodium, and soil texture did not appear to influence the distributional patterns of species associated with this study.

*Eriogonum corymbosum* var. *corymbosum* showed correlation with the above-mentioned factors as well as with total cover. As is evident from the data, *E. corymbosum* var. *corymbosum* prefers areas of low diversity, high shrub cover, shallow soils, high soluble salts, high cation exchange capacities, and low total ground cover. *Eriogonum corymbosum* var. *erectum*, on the other hand, reaches its highest development in communities of high diversity, high grass cover, and deep soils which are low in soluble salts and cation exchange capacities. That both are found on a number of different geological formations supports the hypothesis that this species is an indicator of peculiar soil types.

Other factors involved in the distribution of the above species are competition and community disturbance and erosion. It is suggested that competition between species is probably important because field work indicates, for example, that as the total cover of a community increases, the importance of *E. corymbosum* decreases. Although no measurements were made on community disturbance and erosion, 8 of the 10 study sites showed varying degrees of disturbance and erosion. The 2 sites which did not show erosion but only slight disturbance, indicated by the presence of such plants as *Bromus tectorum* and *Xanthocephalum sarothrae*, also exhibited the lowest composition percents for species such as *E. corymbosum*.

It is suggested that *E. corymbosum* var. *corymbosum*, which is found only in study sites located in the desert areas of the basin, is a shallow soil variety and one that prefers communities that show high degrees of disturbance, little competition, and fairly high levels of soluble salts in the soil and are found at elevations below 5500 feet. *Eriogonym corymbosum* var. *erectum*, on the other hand, appears to compete best in communities above 6000 feet that show less disturbance than the desert areas and have deeper soils and low levels of soluble salts.

Although the suggested associations between the site characteristics measured in this study and the vegetation do not prove causal relationships, they do serve to aid in the assignment of probable causes of the observed vegetational patterns. To gain a complete and final insight into the ecology of *Eriogonum corymbosum* and its associated species of the cold temperate desert shrub regions of the Uinta Basin, further and more intense investigations of those factors studied in this paper, as well as further investigation of other important community characteristics, will be necessary.

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# VARIATION IN HEMOGLOBIN TYPES IN THE DEER MOUSE (*PEROMYSCUS MANICULATUS*) ALONG AN ALTITUDINAL GRADIENT

David Wasserman[1] and Donald J. Nash[1]

Abstract.— Deer mice (*Peromyscus maniculatus*) were captured along an altitudinal gradient that extended from 5,000 feet (1524 m) up to 11,000 feet (3353 m) in central Colorado during August and early September, 1976. Starch gel electrophoresis of deer mouse hemoglobin followed no clear trend that would indicate that slight biochemical differences in the molecule help facilitate adaptation to the decreased $pO_2$ that exists at that altitude.

Organisms that live at high altitudes must in some way adapt to the hypoxic conditions and meet their oxygen needs. Gluecksohn-Waelsch (1960) suggested that multiple hemoglobins may differ in physical properties and thus facilitate environmental adaptations. In one known mutant human hemoglobin, hemoglobin Rainier, on which a histidine residue replaces a tryosine residue at one point, oxygen affinity is greatly enhanced (Stamatoyannopoulos et al., 1968). Studies by Ahl (1968) and Sawin (1970) looked at the electrophoretic patterns found in deer mouse hemoglobin along an altitudinal gradient. In both of these studies a predominance of diffuse (double)-banded individuals were found at low altitude. High altitude groups were characterized by a predominance of single-banded individuals. If the hypothesis put forth by Gluecksohn-Waelsch (1960) is correct, then the patterns discovered in the earlier studies should be found along other altitudinal clines if these biochemical differences in the hemoglobin molecule facilitate greater oxygen-binding efficiency.

## Methods

A total of 67 *Peromyscus maniculatus* were trapped from 27 July through 8 September 1976 in Larimer and Pitkin counties, Colorado, at altitudes of 5,000 feet, 6,500 feet, 8,000 feet, and 11,000 feet. Two populations were sampled at each altitude.

Blood samples were collected from the orbital sinus using heparinized capillary tubes. The blood was centrifuged immediately, and both cells and plasma were frozen with dry ice and later transferred to a freezer and stored at –20 C.

Hemoglobin was analyzed by vertical starch gel electrophoresis, using the method of Smith (1968). Following electrophoresis, gels were sliced, fixed, and stained with bromophenol blue.

## Results and Discussion

A number of studies have dealt with the electrophoretic variants in both the serum and cellular fractions of the blood of the deer mouse. Most studies demonstrated that *Peromyscus maniculatus* has at least two electrophoretically separable hemoglobins (Foreman 1960, Ahl 1968, Sawin 1970). Studies of the genus *Peromyscus* showed that there are variations in the double-banded phenotypes (Rasmussen 1970, Selander et al. 1971). A third hemoglobin variant was reported in one wild mouse captured near Flagstaff, Arizona, in 1967 (McCracken and Foreman 1971). Recent papers have verified the existence of the third variant and three triple-banded phenotypes (Jensen et al. 1976, Maybank and Dawson 1976). It should be noted that the triple-banded individuals were either Foreman's original stock or low altitude populations (600–4700 ft.).

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In previous studies, low altitude deer mice were shown to either have a predominance of individuals exhibiting the diffuse phenotype (type R) or only the diffuse phenotype (Ahl 1968, Sawin 1970). At high altitudes (above 7,000 feet) the single-banded phenotype (type S) was the predominant variety found (Ahl 1968, Sawin 1970). Results of the present investigations do not agree with the previous studies; however, the sampling techniques made it possible to ascertain if the variation found was between altitudes and/or intraaltitudinal in character.

In the populations that were sampled, there was no discernible change in frequencies of the phenotypes over the 6,000 ft. range (Table 1). Population A (5,000 ft. sample) had three individuals that exhibited the single-banded phenotype, but all other individuals in the 5,000 ft. group exhibited the diffuse phenotype. Throughout the remainder of the populations sampled, all individuals exhibited the diffuse phenotype except for two individuals in population I (11,000 feet) that exhibited a triple-banded variety of hemoglobin. It was not possible to ascertain which of the three triple-banded phenotypes as outlined by Jensen et al. (1976) and Maybank and Dawson (1976) was present. It appears to be the first report of the existence of triple-banded hemoglobin phenotypes in high altitude populations.

In light of these findings, the hypothesis put forth by Gleucksohn-Waelsch (1960), which suggests that multiple hemoglobins may differ in physical properties and thus facilitate environmental adaptations, must be questioned. While the two studies noted above found a high frequency of single-banded individuals at higher altitudes, the present results do not follow a similar pattern.

The genetic polymorphisms found along altitudinal gradients could be a product of genetic drift or varying selective pressures in different environments. The findings suggest that the structural variations found in the beta chain of the hemoglobin molecule in *P. maniculatus* do not infer a greater ability on the part of the organism to exist at high altitudes. At the present time it is not known if these slight structural differences manifest themselves in any manner in the deer mouse. The hypothesis put forth by Gleucksohn-Waelsch (1960) could be tested in an alternate fashion by comparing the $O_2$-binding capacities of equal volumes of blood of each phenotype.

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Table 1. Hemoglobin variants and frequencies at trapping sites within altitudes.

| Altitude in feet | Population | Type S | Type R | Type F | Total |
|---|---|---|---|---|---|
| 5000 | A | 3 (.50) | 3 (.50) | – | 6 |
| | E | – | 7 (1.0) | – | 7 |
| 6500 | C | – | 5 (1.0) | – | 5 |
| | D | – | 6 (1.0) | – | 6 |
| 8000 | F | – | 6 (1.0) | – | 6 |
| | G | – | 9 (1.0) | – | 9 |
| 9500 | J | – | 8 (1.0) | – | 8 |
| | K | – | 7 (1.0) | – | 7 |
| 11000 | H | – | 6 (1.0) | – | 6 |
| | I | – | 5 (.70) | 2 (.30) | 7 |

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# FIRST RECORD OF *PATAPIUS SPINOSUS* IN IDAHO AND NEVADA (HEMIPTERA: LEPTOPODIDAE)

Donald R. Brothers[1]

ABSTRACT.— The first record of *Patapius spinosus* (Rossi) in Idaho and Nevada is reported, having previously been found in America only in California.

The family Leptopodidae is represented in America by a single introduced Eastern Hemisphere species, *Patapius spinosus* (Rossi). This species was first reported in America in the United States by Usinger (1941) from a single specimen collected from Colusa County, California. Since that time, it has been collected in a number of California counties in increasing numbers (Drake 1954). To my knowledge, there are no published United States records of *P. spinosus* occurring outside of California. Recent collections of *P. spinosus* from Idaho and Nevada establish the first state record for this insect and represented an eastern extension of its known range. Collection records are as follows:

IDAHO: Gem Co., Pearl vicinity, T6N,R1E,S14, 4400', IX-9-77, IX-14-77, IX-26-77, X-2-77 (D. R. Brothers) (G. A. Shook), adults and nymphs; near Payette River, 12 miles E Emmett, T7N,R1E,S24, 2580', IV-14-78 (G. A. Shook), adults.

NEVADA: Reno, 1971 (M. A. Bechtel).

Although Woodward et al. (1970) reported that leptopodids frequent the drier parts of rocks in streams, it appears that this species may not be restricted to that habitat. Usinger's specimen was found under a piece of fibrous tree protection material on the trunk of an almond tree. Idaho specimens from the Payette River area were taken on the underside of a board in a cottonwood (*Populus*) grove adjacent to the river. Adults and nymphs taken from the vicinity of Pearl were found on the underside of cobble-sized rocks in a mine tailings dump in an area dominated by sagebrush (*Artemisia*) and rabbitbrush (*Chrysothamnus*). The nearest known permanent water from this site is approximately one mile to the west. Adjacent to the site, however, is an intermittent stream which has water for a few months during spring runoff.

Since *P. spinosus* has now been collected east of the Sierras in habitats common to many parts of the Pacific Northwest and Great Basin, it can be anticipated that additional collections of this insect will be made in these areas. Collectors should watch for a small (3–4 mm in length) saldidlike bug with long spines on much of its body, including the eyes (Fig. 1).

Idaho specimens of *P. spinosus* are deposited in the California Academy of Science, San Francisco, California; U.S. Natural Museum, Washington, D.C.; Brigham Young University, Provo, Utah; University of Idaho, Moscow, Idaho; and Boise State University, Boise, Idaho.

## ACKNOWLEDGMENTS

Appreciation is expressed to Dr. Jon L. Herring of the U.S. National Museum for confirming my identification of Idaho specimens and allowing me to report the Nevada record, and to Dr. Charles W. Baker of Boise State University for critically reading the manuscript.

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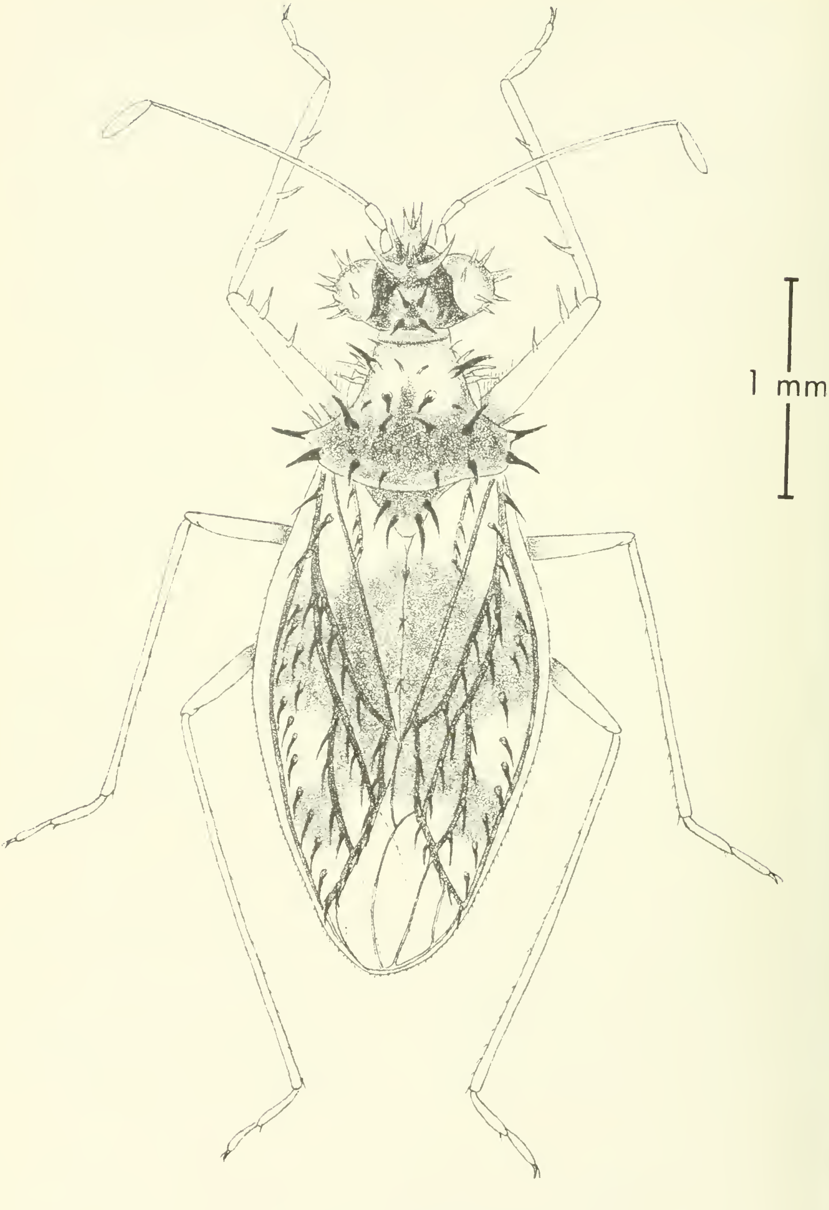

Fig. 1. *Patapius spinosus*, dorsal view.

# BEE VISITATION OF *PHLOX BRYOIDES* (POLEMONIACEAE)

V. J. Tepedino[1,2]

Abstract.— Collections of diurnal insects from a population of *Phlox bryoides* on shortgrass prairie in southeastern Wyoming showed the flowers to be visited predominantly by *Synhalonia fulvitarsis*, a long-tongued bee. Analysis of pollen loads carried by captured bees revealed that almost all individuals were collecting *Phlox* pollen. *P. bryoides* may be an exception to the generalization that the genus *Phlox* is exclusively pollinated by Lepidoptera.

Entomophilous pollination in the genus *Phlox* is thought to be effected almost exclusively by Lepidoptera (Grant and Grant 1965). Species with corollas 1–2 cm long are exclusively pollinated by perching butterflies; those with corollas 3–4 cm long are pollinated by hawkmoths (Grant and Grant 1965). Based upon observations of three species (*P. caespitosa* Nutt., *P. diffusa* Benth., *P. multiflora* A. Nels.) plus a citation for *P. andicola* (Britt.) (Wherry 1955), it was concluded that all species of the Section Occidentales (=Section Microphlox of Wherry 1955), which "contains over 20 species of woody-based, needle-leaved, cespitose or cushion-like shrubs," were pollinated by Lepidoptera (Grant and Grant 1965). In particular, western cushion plants with erect 1-cm-long corolla tubes are pollinated by perching noctuid moths (Grant and Grant 1965). However, at least two species in the Section Occidentales possess corollas that are substantially shorter than 1 cm (*P. bryoides* Nutt., *P. hoodii* Rich., measurements from Wherry 1955) and could be pollinated by long-tongued bees or flies. Indeed, data reported here from a population of *P. bryoides*, a dense cushion plant common on shallow soils and rocky outcrops in southeastern Wyoming, suggest that the Grants' general conclusion (1965) may require modification. Individuals of the long-tongued eucerine bee species *Synhalonia fulvitarsis fulvitarsis* (Cresson) were common pollen collectors on the flowers and may be important pollinators.

*Phlox bryoides* blooms from the last half of May to late June/early July, with peak flowering during the first half of June. During this period in 1975 and 1976, weekly collections of flower-visiting bees were made during four hour-long periods, two each in morning and afternoon, on an 11000-m$^2$ plot in Albany Co., 8 km SSE of Laramie. About 30 percent of the plot was covered heavily by *P. bryoides*. Collections were not restricted to *P. bryoides*; rather, each floral species was censused in rough proportion to its percent of total floral abundance during each period. Thus the number of insects visiting *P. bryoides* was much larger than the relatively small numbers reported here.

*Synhalonia fulvitarsis* works the salverform flowers of *P. bryoides* very rapidly, visiting only a few of the many available in each cushion before moving to another cushion. In 1975, 11 females, 10 carrying pollen, were captured on the flowers of *P. bryoides*; in 1976 7 of 8 females captured had *Phlox* pollen loads. No diurnal pattern in foraging was evident except that females did not begin visiting flowers until after 1030 hours. Thereafter, activity was evenly spaced until collection ended, generally between 1530 and 1600 hours. Other bee species found on *Phlox* were represented by only 1 or 2 individuals each, and they did not carry pollen. Diurnal Lepidoptera were rare on the flowers.

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Most pollen loads examined from the 17 specimens (both years combined) contained more than 70 percent *Phlox* pollen (Fig. 1). Indeed, seven females carried loads that were almost pure (90 percent *Phlox* or higher), and the mean for all pollen loads was 64.5 percent *Phlox* (S. D. = 35.4, range 5.6–100.0).

Although Timberlake (1969) also reported S. *fulvitarsis* from the flowers of *Phlox*, this association does not appear to be obligatory. Rather S. *fulvitarsis* is probably polylectic, because it has been recorded from a large number of plant species (Timberlake 1969).

Effective cross-pollination in the Section Occidentales seems to require a nectar rather than pollen-collecting flower visitor because the anthers are situated above the stigma while the nectaries are located at the base of the corolla tube (Grant and Grant 1965). Thus, species that collect only pollen would not contact the stigma. In most species of *Phlox* the length of the corolla tube precludes nectar collection by all but long-tongued Lepidoptera. In *P. bryoides*, however, (and in *P. hoodii* as well) the corolla tube is relatively short (4–8 mm, Wherry 1955) and the nectaries are well within the reach of long-tongued bee species such as S. *fulvitarsis* (proboscis length measured from base of mentum through flabellum; $\bar{x} = 8.44$, s.d. = 0.465, N = 20 ♀ ♀). It is not unlikely that S. *fulvitarsis* collects nectar from *P. bryoides* at the same time pollen is collected, thereby achieving pollination. Whether *P. bryoides* is dependent upon long-tongued bees for pollination in any consistent way awaits the examinations of other populations.

Although bee pollination is prevalent in the family Polemoniaceae, it is regarded as the primitive condition from which all other pollination systems have been derived (Grant and Grant 1965). Moreover, the genus *Phlox* is regarded as an advanced member of the family, in part because of its pollination syndromes (Grant and Grant 1965). Wherry (1955) viewed Microphlox as an advanced section of the genus *Phlox* on morphological grounds and regarded the subsection Canescentes, of which *P. bryoides* and *hoodii* are members, as perhaps the most advanced group in the Microphlox. If both interpretations are correct, then bee pollination in the Canescentes represents reversion to the primitive condition in an advanced branch of the family.

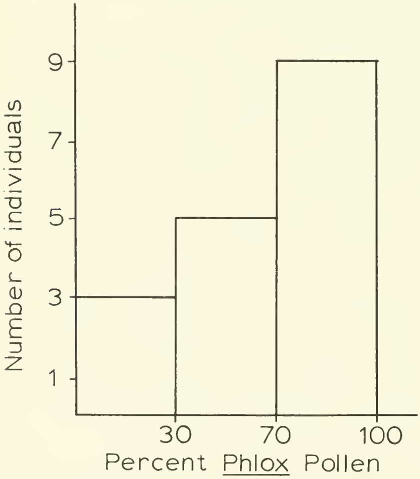

Fig. 1. Distribution of pollen loads carried by *Synhalonia fulvitarsis* by percent *Phlox bryoides*.

## ACKNOWLEDGMENTS

I appreciate the helpful suggestions on the manuscript provided by Verne Grant, Arthur Holmgren, and P. F. Torchio.

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# ECOLOGICAL DISTRIBUTION OF RODENTS IN CANYONLANDS NATIONAL PARK, UTAH

David M. Armstrong[1]

ABSTRACT.— Studies of microhabitat of 14 species of rodents by cluster analysis suggested that the diverse landscapes of Canyonlands National Park, Utah, include six broad "habitat-types": (1) rimrock; (2) desert shrublands; (3) saxicoline woodland and sagebrush; (4) oakbrush; (5) riparian deciduous woodland; and (6) grasslands. *Perognathus parvus* and *Neotoma cinerea* were the species most strongly associated with single "habitat-types," desert shrub and saxicoline woodland, respectively. *Peromyscus maniculatus* and *P. truei* were the species associated with the broadest ranges of habitats. The rodents with the most similar habitats were *Neotoma mexicana* and *Peromyscus boylii*; *Eutamias quadrivittatus, P. truei,* and *P. crinitus*; *Ammospermophilus leucurus* and *P. maniculatus*; and *Dipodomys ordii* and *Onychomys leucogaster.*

An understanding of ecological distribution of organisms is important for both interpretation and management of ecosystems. Typically the vertebrate ecologist describes patterns of ecological distribution in terms of vegetational associations recognized *a priori.* The purpose of this paper is to allow the rodent fauna itself to define salient patterns of environmental features in Canyonlands National Park and meaningful associations of mammalian species. This not only provides a description of environmental patterns, but allows field naturalists to check their sense of the landscape against mammalian habitats, rather than the opposite (i.e., forcing species' distributions into their view of environmental pattern).

Canyonlands National Park preserves some 450 square miles (1170 km$^2$) of spectacular canyons and mesas in San Juan and Wayne counties, southeastern Utah. The park includes the confluence of the Green and Colorado rivers, which are entrenched in canyons up to 2000 ft. (610 m) deep. These canyons divide the park (and the rest of southeastern Utah) into three distinct land masses. Elevations in the park range from about 3750 to nearly 7000 feet (1150–2135 m). This range of relief dictates a wide variety of physical conditions and a complex distribution of biotic communities.

Knowledge of mammals of the Canyonlands is rather scanty. The area was ignored by the exploratory parties that provided fundamental knowledge of mammalian distribution elsewhere in the West, such as the Railroad Surveys of the 1850s and the Bureau of Biological Survey in the early 1900s. John Wesley Powell's expeditions of the 1870s paid almost no attention to the biota of the region. Although the U.S.-IBP Desert Biome Project worked over much of the desert Southwest, no study area was located on the Colorado Plateau (MacMahon 1976).

The Canyonlands Section of the Colorado Plateau physiographic province is a showcase for the effects of erosion on an arid land dominated by flat-lying sedimentary strata. For details of geology, see Baars (1971) and Lohman (1974). The climate of Canyonlands is arid, with hot summers, cold winters, and pronounced diel fluctuations in temperature. Mean annual precipitation is about 7.5 in., about one-third of which falls during the third quarter of the year, usually as local, torrential thunderstorms (Tanner 1965). Excepting the immediate vicinity of the master streams, perennial surface water is limited to a few widely scattered springs and seeps. Bare rock comprises more than half of the surface. Where soils have formed, they are reddish, gravelly to silty loams, moderately alkaline in reaction (Wilson et al. 1975). Undeveloped aeolian sands and silts are present locally.

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Vegetation of the Canyonlands varies widely with physiographic setting, edaphic conditions, available moisture, and grazing history. Hayward et al. (1958) described four principal vegetation types in the vicinity of Arches National Park: (1) cottonwood-willow-tamarisk floodplain, (2) northern desert shrub, (3) pinyon-juniper woodland, and (4) hanging gardens. Although dominance changes locally, these types point out associations that are recognizable in the landscape (and are reflected in mammalian distributions to some extent). On relatively stable interfluves, thin, silty soils form. Such flats and rockbound parks are clothed with grassland. *Oryzopsis*, *Hilaria*, *Stipa*, *Sporobolus*, and *Bouteloua* are important genera of grasses; *Yucca*, *Opuntia*, *Gutierrezia*, and a variety of annual forbs are present also. Areas of rimrock, slickrock, and canyon walls are a frequent topographic type. These areas often are precipitous; typical substrate is a coarse, unstable colluvial rubble. Vegetation on such sites includes a variety of shrubs, among them *Cowania* and *Shepherdia* on slopes, and *Mahonia* and *Quercus* at bases of cliffs. Woodland of juniper or juniper and pinyon occurs locally on such sites and also on well-drained mesa tops. The understory in this community varies, apparently with edaphic conditions. Phreatophytic cottonwoods (*Populus*) and willows (*Salix*) or exotic saltcedar (*Tamarix*) occur along the major washes. Floodplains support stands of halophytic shrubs (*Sarcobatus*, *Atriplex*). Sagebrush (*Artemisia*) often occurs in association with junipers or as an overstory on grassy flats. "Hanging gardens" develop locally as mesic associations watered by seepage at contacts between some rock units. These associations are comprised of a striking variety of plants, including *Mimulus*, *Aquilegia*, *Habenaria*, and *Rhus*.

Despite generally forbidding physical conditions, Canyonlands National Park supports a diverse vertebrate fauna, including some 60 species of mammals. For general information on the region as a whole, see Hayward et al. (1958). Tanner (1965) provided notes on a few species of rodents. Durrant and Dean (1959) commented briefly on ecological distribution of rodents in Glen Canyon (now inundated by Lake Powell), immediately south of Canyonlands. Johnson (1976) and Clevenger (1977) have presented data on some aspects of ecology of rodents in Canyonlands National Park. For further information on mammals of southeastern Utah, see Benson (1935), Durrant (1952), Durrant and Dean (1959), Kelson (1951), Lee (1960), and Armstrong (1977b, in press).

This report concerns 14 species of rodents, most of them abundant and widespread (vernacular name, sample size in parentheses): *Eutamias quadrivittatus* (Colorado chipmunk, 64), *Ammospermophilus leucurus* (white-tailed antelope squirrel, 23), *Perognathus apache* (Apache pocket mouse, 29), *P. parvus* (Great Basin pocket mouse, 35), *Dipodomys ordii* (Ord's kangaroo rat, 88), *Reithrodontomys megalotis* (western harvest mouse, 24), *Peromyscus crinitus* (canyon mouse, 124), *P. maniculatus* (deer mouse, 128), *P. boylii* (brush mouse, 82), *P. truei* (pinyon mouse, 202), *Onychomys leucogaster* (northern grasshopper mouse, 49), *Neotoma mexicana* (Mexican woodrat, 45), *N. lepida* (desert woodrat, 34), and *N. cinerea* (bushy-tailed woodrat, 20). Rodents represented by too few specimens for analysis are *Spermophilus variegatus*, *Thomomys bottae*, *Castor canadensis*, *Neotoma albigula*, and *Erethizon dorsatum*.

## METHODS

Field work on mammals of Canyonlands National Park began in 1972 and continued intermittently to 1978, the principal aim being to provide a range of data on natural history basic to a popular account of the fauna for the National Park Service. Given the broad aims of the research program of which this report is a part, data were gathered by various means. Whatever the source of a specimen, its habitat was described as the most prominent feature of plant cover within 1 m of the trap. When no plant was within this radius, a physical descriptor of the trapsite was noted. Analysis of data follows the method utilized by Armstrong (1977a). The similarity index used is $P_C/P_A + P_B$, where $P_C$ is the sum of percentage occurrences in common, and $P_A$ and $P_B$ are percentage occurrences of the two descriptors under comparison. Use of relative (rather than absolute) frequency obviates some problems of differences in sample size. Cluster analysis was by the unweighted pair-group method of Sokal and Sneath (1963:309). Specimens collected in the course of this work are housed in the University of Colorado Museum.

## RESULTS AND DISCUSSION

Analysis of data was designed to answer three kinds of questions: (1) What associations of habitat descriptors have reality to the rodent fauna? (2) How broadly distributed are species across those "habitat types"? (3) What associations of rodents are found in given habitats? An answer to the first question should approximate a "mouse's-eye view" of the mosaic of habitats. The second question approaches the phenomenon of fidelity; how faithful are rodents to their habitat? Reasonable answers here could be quite helpful in making predictive statements about habitat management. Answers to the third question suggest groups of species that may be worthy of further study from the standpoint of niche structure or competitive interactions.

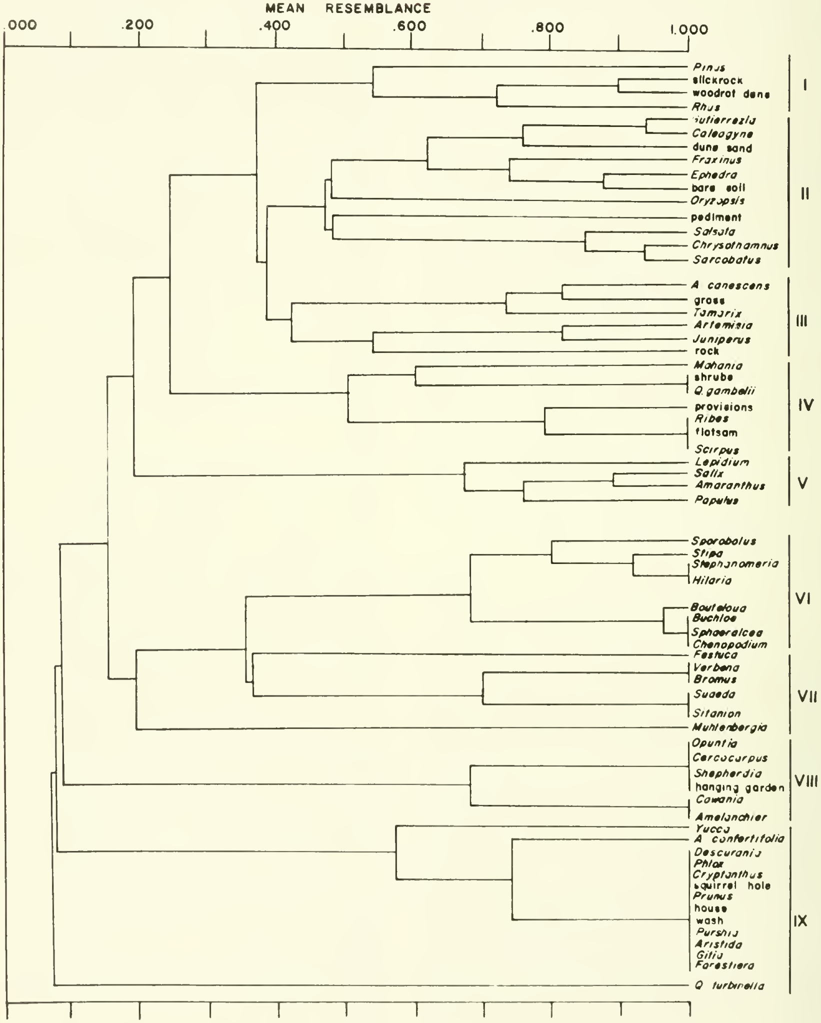
Figure 1 is a cluster diagram of 66 descriptors of habitat, based on indices of similarity of rodents associated with each descriptor. Overall mean similarity in the matrix upon which this diagram was based was 0.1783. Taking a mean similarity of 0.450 as an arbitrary cut-off point, there are nine major subclusters of descriptors in the diagram. Group I includes descriptors of slickrock and rimrock areas, including woodrat dens, most of which are beneath rocky rims. Group II includes many descriptors of open shrublands with poorly developed soils and silty blowouts or dune sand. Group III is quite complex; it includes descriptors of juniper woodland and broken rocky habitats as well as sagebrush stands. Saltbush and tamarisk also appear in this subcluster. Group IV centers around Gambel's oak and represents the relatively mesic brushlands common at bases of cliffs in the Cave Springs area of the Needles District. Group V describes phreatophytic cottonwood-willow woodland of major washes and canyon bottoms.

Group VI includes grasses and forbs typical of open flats. Groups VII, VIII, and IX are closely related neither to each other nor to other subclusters. All represent descriptors with small samples of rodents associated. The closest resemblance of subcluster VII is with group VI; both groups describe grasslands. Groups VIII and IX truly are miscellaneous, although group VIII does include several descriptors of relatively mesic cliffside habitats: *Cowania*, *Cercocarpus*, *Amelanchier*, hanging gardens.

These subclusters form a complex pattern, not as nearly comformable as one might hope with the sorts of habitat-types that have been described by previous workers (e.g., Hayward et al. 1958), or the units that the field naturalist extrapolates from the landscape. One reason for this is the great ecological amplitude of the most abundant species in the sample, *Peromyscus truei*, which is about equally abundant in sagebrush and in juniper stands.

Figure 2 indicates the cumulative percentage distribution of each rodent species with respect to the nine major subclusters identified in Figure 1. This allows a look at the degree of fidelity of species to certain environmental attributes. First, note that all species have an association with a single subcluster of descriptors of greater than 40 percent; indeed, all species except *R. megalotis*, *P. maniculatus*, and *P. crinitus* show primary associations of greater than 50 percent.

Five species, *A. leucurus*, *P. parvus*, *D. ordii*, *R. megalotis*, and *O. leucogaster*, show a primary association with subcluster II, representative of open shrublands on silty to sandy soils. Of these, *A. leucurus* also shows relatively strong secondary associations with groups I and III. Most often, antelope ground squirrels occur in the narrow ecotone between rocky situations and desert flats. *D. ordii* shows strong secondary association with group III. This is due to its frequent occurrence in stands of sagebrush. *Reithrodontomys megalotis* also has a strong secondary association with group III; harvest mice usually are found on floodplains which may have cover of greasewood (Group II), saltbush or tamarisk (group III) or phreatophytic woodland (Group V). *Onychomys leucogaster* is similar in local distribution to *D. ordii* (also see Fig. 3, beyond). The species most strongly associated with group II is *P. parvus*, a species found only in the Maze District. This species is known from a wide variety of habitats in Utah (Hayward and Killpack 1958), but does not seem to be particularly euryecious in the park, occurring mostly under sparse cover of blackbrush (but on a variety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Coleogyne
dune sand
Fraxinus
Ephedra
bare soil
Oryzopsis
pediment
Salsola
Chrysothamnus
Sarcobatus
A canescens
grass
Tamarix
Artemisia
Juniperus
rock
Mahonia
shrubs
Q gambelii
provisions
Ribes
flotsam
Scirpus
Lepidium
Salix
Amaranthus
Populus
Sporobolus
Stipa
Stephanomeria
Hilaria
Bouteloua
Buchloe
Sphaeralcea
Chenopodium
Festuca
Verbena
Bromus
Suaeda
Sitanion
Muhlenbergia
Opuntia
Cercocarpus
Shepherdia
hanging garden
Cowania
Amelanchier
Yucca
A confertifolia
Descurania
Phlox
Cryptanthus
squirrel hole
Prunus
house
wash
Purshia
Aristida
Gilia
Forestiera
Q turbinella
I
II
III
IV
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VII
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IX

Fig. 1. Cluster diagram of 66 habitat descriptors, based on similarity of associated species of rodents. Abbreviations: A., *Atriplex*, Q., *Quercus* (for explanation of index, see text).

of substrates, from dune sand to cobbly desert pavement). Only *P. apache* shows a primary association with group VI, which describes grassland. The Apache pocket mouse is considerably more stenoecious than its larger congener, *P. parvus*, being closely restricted to bunchgrass flats on sandy to silty soils.

All four species of *Peromyscus* show their primary association with group III, rocky habitats. Three of the four show strongest secondary association with subcluster II, shrublands; *P. boylii* is the exception, with a strong secondary association with oak brush (Group IV). This analysis is sufficiently crude that it tends to make these species look more similar in ecological distribution than they may actually be. It is not at all uncommon to take three or even four species of *Peromyscus* in adjacent traps, particularly in broken country. Frequently the animals occur in "text-book" fashion: *P. crinitus* on slickrock, *P. maniculatus* in open shrubs, *P. boylii* beneath oakbrush, and *P. truei* with junipers. These relationships are partially obscured in the present analysis by data from localities at which fewer species co-occur or in which environments are too complex for the methods used. It is a seeming paradox that no species of *Neotoma* is related strongly with Group I, which includes the descriptor "woodrat dens." This reflects the fact that woodrats are more difficult to trap in the immediate vicinity of their dens than on their foraging range away from the den. Figure 2 suggests that *N. lepida* is the most euryecious of local species of *Neotoma*, although all species have strong primary associations with subcluster III.

Figure 3 is a cluster diagram of similarity indices of 14 species of rodents with respect to descriptors of habitat. Mean resemblance

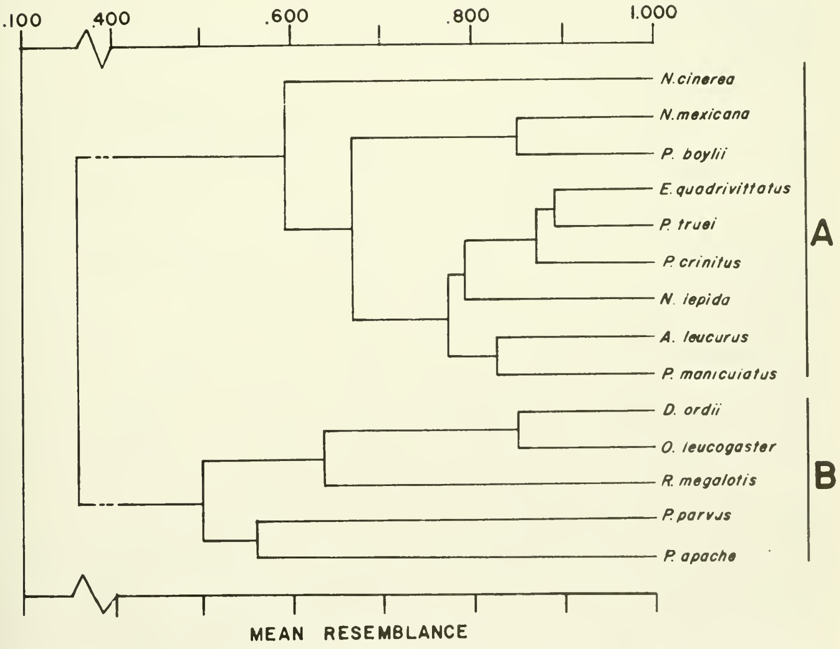

Fig. 2. Cumulative percentage distribution of 14 species of rodents with respect to nine subclusters of habitat descriptors.

in the similarity matrix on which the diagram was based is 0.5297. The diagram shows two different "habitat groups" of rodents, one (group A) occupying broken, rocky habitats, the other (group B) restricted to flats with relatively well-developed soils. The strongest associations are between *N. mexicana* and *P. boylii, E. quadrivittatus, P. truei,* and *P. crinitus, A. leucurus* and *P. maniculatus,* and *D. ordii* and *O. leucogaster. Neotoma mexicana* and *P. boylii* co-occur regularly in saxicoline oakbrush and *Mahonia* thickets in the Needles District. *Eutamias quadrivittatus, P. truei,* and *P. crinitus* occur in rough, broken terrain, *P. truei* most often in scattered juniper woodland, *P. crinitus* more frequently in more open situations. *Peromyscus maniculatus* and *A. leucurus,* which are related closely to the saxicolous group, are species that occupy the ecotone between the two broad habitats; they seem to be about equally likely to be captured among rocks or in open country. *Dipodomys ordii* and *O. leucogaster* occur in open shrub- or grassland on sandy soils. The pattern of dispersion across groups of descriptors in Figure 2 suggests that *P. truei* and *P. maniculatus* are the most euryecious of local rodents. They also are the species with the highest mean habitat similarity to all other species, 0.702 and 0.672, respectively.

Perhaps the most striking feature of the foregoing analyses is the strong microhabitat similarities among the saxicoline rodents.

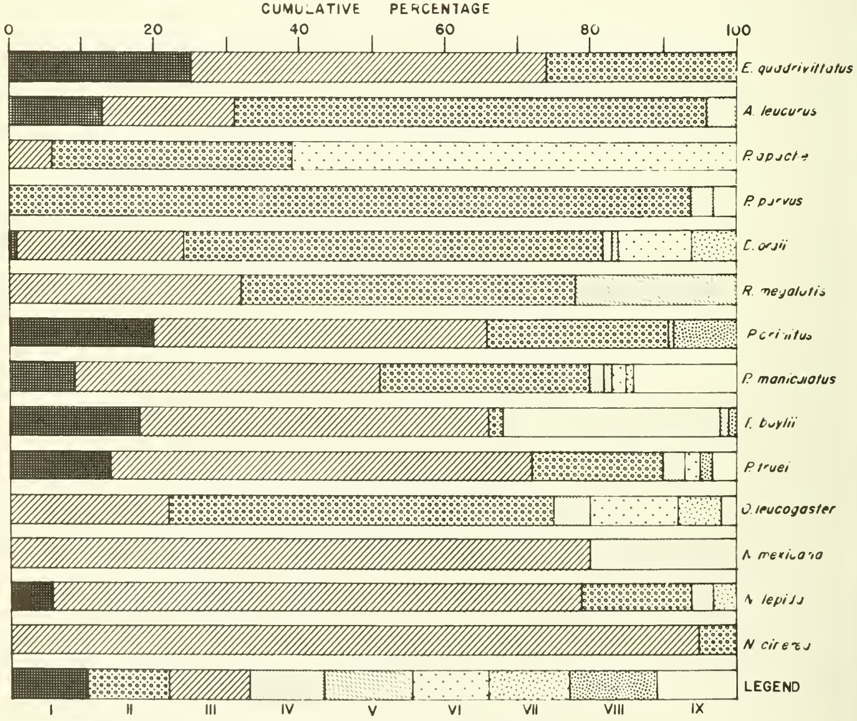

Fig. 3. Cluster analysis of indices of similarity of 14 species of rodents with respect to descriptors of habitat (for explanation of index, see text).

This is especially noteworthy among closely related species of cricetines, *Peromyscus* and *Neotoma*. Other criteria by which these species assort resources to allow coexistence are under study.

The only previous study of ecological distribution of rodents in the general vicinity of Canyonlands National Park was that by Hayward et al. (1958), who reported on Arches National Monument as one of several study areas. The suite of species considered was slightly different (*Thomomys bottae* was included, but neither *P. parvus* nor *N. mexicana* was) and the approach was geographically broader and more anecdotal. Still, correspondence with results of the present study is close. Hayward et al. (1958:32, Fig. 16) showed *E. quadrivittatus*, *A. leucurus*, and *P. truei* as considerably more stenoecious than they are in Canyonlands. They pointed out that *N. lepida* is more broadly distributed ecologically than is *N. cinerea*, a fact suggested by our data.

## ACKNOWLEDGMENTS

Several people and organizations have contributed to the study of the mammals of Canyonlands National Park. David May, chief naturalist, encouraged the work and has provided logistic support. Among National Park Service personnel, David W. Johnson, Peggy Johnson, David Harwood, and Walter Loope deserve special thanks for their help in the field. Charles L. Curlee, James G. Owen, S. Scott Panter, and William C. Sears provided field assistance, and Michael Johnson and James C. Halfpenny did considerable independent field work as graduate research assistants. My family, Ann, Jack, and Laura, deserve recognition not only for their help with field work but also for consenting to live in the field for several months. Financial support has been provided by the Society of the Sigma Xi (1972), a Summer Research Initiation Faculty Fellowship from the Council on Research and Creative Work of the University of Colorado (1973), the Penrose Fund (Grant 7615) of the American Philosophical Society (1976), and the Colorado State University National Park Service Cooperative Studies Unit (1977 and 1978).

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## TABLE OF CONTENTS

Review of tularemia in Utah and the Great Basin. Harold E. Stark ........ 103

Chemical composition of some important plants of southeastern Utah summer ranges related to mule deer reproduction. Jordan C. Pederson and K. T. Harper ........ 122

Emergence data and artificial rearing media for an aspen bark beetle, *Trypophloeus populi* (Coleoptera: Scolytidae). David A. Stewart, Gary M. Booth, Jerold L. Petty ........ 129

New synonymy and new species of American bark beetles (Coleoptera: Scolytidae), Part VIII. Stephen L. Wood ........ 133

Annual energy budgets for three common rodent species in the northern Great Basin. R. Kent Schreiber ........ 143

Preliminary survey of raptor species in the Manti Division, Manti-LaSal National Forest. Stephen G. Jones ........ 155

Vegetation response to a moisture gradient on an ephemeral stream in central Arizona. Deborah Ann Bloss and Jack D. Brotherson ........ 161

Ecological and community relationships of *Eriogonum corymbosum* (Polygonaceae) in the Uinta Basin, Utah. Jack D. Brotherson and Karen J. Brotherson ........ 177

Variation in hemoglobin types in the deer mouse (*Peromyscus maniculatus*) along an altitudinal gradient. David Wasserman and Donald J. Nash ........ 192

First record of *Patapius spinosus* in Idaho and Nevada (Hemiptera: Leptopodidae). Donald R. Brothers ........ 195

Bee visitation of *Phlox bryoides* (Polemoniaceae). V. J. Tepedino ........ 197

Ecological distribution of rodents in Canyonlands National Park, Utah. David M. Armstrong ........ 199

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11-79 650 42594

# The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 39 | September 30, 1979 | No. 3

## VEGETATIVE AND EDAPHIC FACTORS AFFECTING ABUNDANCE AND DISTRIBUTION OF SMALL MAMMALS IN SOUTHEAST OREGON

George A. Feldhamer[1]

ABSTRACT.— The relationships between vegetative and edaphic habitat factors and the local distribution and abundance of small mammals on Malheur National Wildlife Refuge, Harney County, Oregon, were examined between July 1973 and June 1975. Of 16 species of small mammals captured, deer mice (*Peromyscus maniculatus*), montane voles (*Microtus montanus*), Great Basin pocket mice (*Perognathus parvus*), and least chipmunks (*Eutamias minimus*) comprised 90.1 percent of the individuals. The physiognomy of the vegetation was a factor in the distribution of rodent species other than deer mice. Pocket mice and chipmunks were restricted to the communities dominated by sagebrush (*Artemisia tridentata*) or greasewood (*Sarcobatus vermiculatus*). Population densities of pocket mice and chipmunks were significantly related to edaphic factors such as soil depth, texture, and strength, which may have affected the construction and stability of burrows. Montane voles occurred only in marsh or grassland communities. Population densities of voles were directly correlated with the amount of cover and inversely correlated with its patchiness. Deer mice were the most common species encountered and occurred in all but the grassland communities. The density of this species was related to vegetative or edaphic factors only seasonally or in certain habitats, and few generalizations could be made.

The general habitat preferences of many species of small mammals have been documented by several generations of natural historians, and often can be attributed to food preferences and associated morphological adaptations (Baker 1971). Many other extrinsic factors affect populations of small mammals, including vegetation, soils, predation, competition, and weather. Intrinsic factors, such as genetic and behavioral changes, also are of significance (Krebs 1964:63–67). However, the quantitative relationships between many environmental factors and the distribution and abundance of small mammals usually are considerably less well known than their general preferences.

This study was initiated to provide quantitative information concerning the effect of vegetative and edaphic factors on the local distribution and abundance of small mammals inhabiting four community types on the Malheur National Wildlife Refuge.

### DESCRIPTION OF THE AREA

Malheur National Wildlife Refuge is primarily a resting and breeding area for migratory waterfowl and is located in the Harney Basin, Harney County, Oregon, between 118.5° and 119.5° W longitude and 42.7° and 43.4° N. latitude (Fig. 1). The refuge is at an elevation of approximately 1250 meters (m). The climate is characterized by dry summers with temperatures rarely exceeding 32.2 C and cold winters with average temperatures of –6.6 C. The average annual precipitation is 22.9 cm, much of which occurs as snowfall (Meteorology Committee, Pacific Northwest River Basin Commission 1969).

Much of the refuge consists of valley wetlands vegetated primarily by hardstem bulrush (*Scirpus acutus*), cattail (*Typha latifolia*), baltic rush (*Juncus balticus*), sedges (*Carex* sp.), and submerged and emergent wetland flora. Rimrock areas above the valley floor support mainly big sagebrush, greasewood, and grasses, principally the exotic annual, cheatgrass (*Bromus tectorum*). Grassland areas were dominated by bluegrass (*Poa secunda*), saltgrass (*Distichlis stricta*), bluestem (*Agropyron smithii*), and numerous other graminoid species, as well as sedges.

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## Methods and Materials

Eighteen study plots were established among the four predominant types of terrestrial plant communities on the refuge. Five plots each were in sagebrush and greasewood areas and four plots each were in marsh and grassland communities. Areas designated as marsh were characterized by habitat factors that generally conformed to the "inland shallow fresh marsh" category of Shaw and Fredine (1956:21). Areas designated as grassland conformed to the "inland fresh meadow" category. Live-trapping on all plots was conducted once during 1973 (July–September), twice in 1974 (June–August, September–November), and once in 1975 (April–June). Each trapping period roughly corresponded seasonally to either spring, summer, or fall, except in 1973. Vegetative and edaphic parameters were measured during each trapping period.

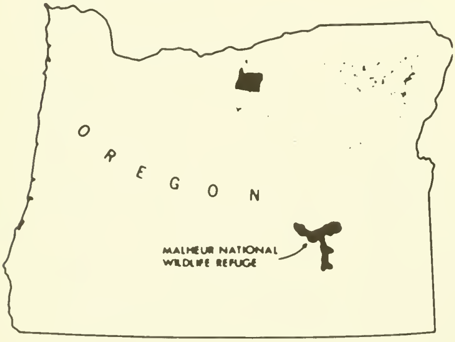

Fig. 1. Location of Malheur National Wildlife Refuge, Harney County, Oregon.

## Small Mammals

Trapping grids consisted of 49 Sherman live-traps at 15.0 m intervals in a square grid of 1.1 ha (2.7 acres). This area included a border of 0.3 ha (0.7 acres), from which it was assumed animals would be captured (Faust et al. 1971).

Traps were operated for 10 consecutive days, except during 1973, when grids were operated for 3- or 4-day periods. Traps were baited with rolled oats, contained Dacron batting for nesting material, and were covered with aluminum shields to minimize heat stress (Feldhamer 1977). Animals were removed from traps as soon after dawn as possible.

Trapped animals were individually marked by toe clipping, following the procedure outlined by Taber and Cowan (1971), and released at their respective points of capture. The species, sex, reproductive condition, age class, weight, and trap locality of each captured animal were recorded.

Reproductively active males had descended testes. Females were termed pregnant if their abdomens were visibly swollen or if developing young were detected by palpation. Nursing females were recognized by lacking fur around the teats or by large and protruding mammae.

Individuals were classified as juvenile or adult on the basis of body size and weight. All deer mice (*Peromyscus maniculatus*) with grey pelage or an incomplete postjuvenile developmental molt were considered juveniles (Layne 1968). The estimated mean densities during each trapping period, and associated estimates of variance, were calculated using a Mean Peterson Estimate (Seber 1973:138). The trap-revealed distribution of the four common species inhabiting the study plots were classified as uniform, random, or clumped by Southwood's (1966:36) index of dispersion ($X^2$).

## Vegetation

Percentage cover was estimated on each plot using a Gossen Tri-Lux photoelectric cell. Light intensity was measured between 1100 and 1300 hours at ground level and immediately above the vegetation at each of 10 points. The percentage differences between readings represented the amount of cover at each point. Measurements were made at 20 m intervals along two diagonal transects on each plot and the average considered an index to the cover present during that trapping period. In addition, in 1975 each plot was visually "divided" into 49 quadrats, each 15.0 $m^2$ with a trap-site at the center. The percentage of cover in each quadrat was estimated and rated as follows: 0–20 percent = 1; 21–40 percent = 2; 41–60 percent = 3; 61–80 percent = 4; and 81–100 percent = 5 (Myton 1974). For each species of small mammals, a chi-square ratio test was used to determine if the number of captures were equal for each of the five ratings. Expected values were calculated as—

$$E\ (\text{captures/rating } i) = \frac{\text{total captures on plot}}{\text{trap sites}}\ (\text{number of sites with rating } i)$$

These distributions were considered separately for each plot.

Although an average cover value was calculated for each plot, individual portions often differed substantially in the amount of cover present. Therefore, the same five-division rating system (Myton 1974) was used to calculate a cover diversity index ("patchiness") from the 10 photometric cover readings made on each plot. The formula $1/\Sigma q_i^2$ was used (M'Closkey and Fieldwick 1975) where $q_i$ was the proportion of readings within each of the five cover rankings.

During the initial trapping period on each plot in 1974, the foliage height diversity (FHD) of the vegetation was measured using general methods described previously (MacArthur and MacArthur 1961, Rosenzweig and Winakur 1969, M'Closkey and Lajoie 1975). Vegetative density was measured in a different direction from each of the eight central trap-stations at heights of 7.6, 15.0, 30.0, 46.0, and 61.0 cm above the ground ($q_i$). The FHD was computed using $1/\Sigma q_i^2$, with i = 1, 3, and 5 only. Thus, the vegetation was considered to occupy three distinct layers: below 15.0 cm, between 15.0 and 46.0 cm, and above 46.0 cm.

The percentage of vegetative moisture (succulence) was determined each trapping period beginning in 1974. Ten samples were collected at 20 m intervals along two diagonal transects and an average succulence value per plot computed. The procedure involved clipping vegetation from an approximate 1 -$m^2$ area, placing samples in airtight cans, and weighing each sample before and after oven drying at about 63 C to determine the weight of water in the material. The ratio of water weight to dry weight was considered the percent moisture content (Dawson 1972).

## Soils

The soil texture of each study plot was determined once in 1973 and was considered to remain constant for the duration of the field work. Ten soil subsamples were collected from depths of approximately 15.0 cm along diagonal transects. Subsamples were combined to form a single sample that was analyzed for composition of sand, silt, and clay using the Bouyoucos method (Dawson 1971).

The mean soil depth on each plot was estimated by forcing a sharpened steel probe, 1.0 cm in diameter, into the ground to a depth of 102.0 cm. If an obstruction was met prior to this depth, the distance from ground surface to the obstruction was recorded. An average depth was determined from 10 probings made along diagonal transects.

The soil sheer stress ("strength") on each plot was measured once during the initial trapping period of 1974, using a Soil Test pocket penetrometer. The index value, measured in kg/$cm^2$, was in direct proportion to the soil strength. Ten measurements, made along diagonal transects, were averaged to obtain a mean value. Diversity values for both soil depth and soil strength were calculated using $1/\Sigma q_i^2$. For soil depth, diversity was computed on the basis of four equal rankings ($q_i$) of 25.4 cm each. Diversity for soil strength also was computed on the basis of four rankings: 0–1.12, 1.12–2.25, 2.26–3.39, and 3.40–4.50 kg/$cm^2$.

The percentage soil moisture on each plot was estimated each trapping period following the procedure described to estimate vegetative succulence. Ten samples were collected from a depth of 15.0 cm along diagonal transects and an average value computed.

### Regression Analyses

Linear regression analyses were used to determine the relationship between the estimated mean density of each species of small mammal and concurrently measured independent habitat parameters. Habitat variables and associated densities of small mammal species in each of the four community types were analyzed in three groupings: (1) for the entire study period; (2) for all periods exclusive of 1973, so that the effects of vegetative succulence and patchiness could be evaluated; and (3) for the initial trapping period of 1974, because foliage height diversity and soil strength were measured only during this period. Correlations were considered to be statistically significant if $P<0.05$.

## RESULTS AND DISCUSSION

During the field work, 26,460 trap-nights on the study plots produced 4,717 captures of small mammals. These captures involved 1,580 individuals and represented four mammalian orders (Table 1). Three orders were represented by single species and were considered incidental to the study because traps were not set for them. Although 13 species of rodents from four families were captured, deer mice, montane voles (*Microtus montanus*), Great Basin pocket mice (*Perognathus parvus*), and least chipmunks (*Eutamias minimus*) comprised 90.1 percent of the small mammals captured and were considered in detail in the analyses and discussion. All four species had trap-revealed sex ratios significantly biased toward males ($P<0.05$). Male-to-female ratios were: deer mice, 1.7:1.00; montane voles, 2.12:1.00; Great Basin pocket mice, 1.7:1.00; and least chipmunks, 1.9:1.00.

### *Perognathus parvus*

*Density.*— Great Basin pocket mice were resident only in sagebrush or greasewood communities. In sagebrush communities, among-plot variation in the density of pocket mice differed seasonally only by a factor of about 4. Within-plot variation did not exceed

TABLE 1. Total number of individuals of each mammalian species captured on study plots in the four predominant types of terrestrial plant communities on Malheur National Wildlife Refuge from July 1973 through June 1975.

| | | Community Type | | | | |
|---|---|---|---|---|---|---|
| Order | Species | Sagebrush[a] | Greasewood[b] | Marsh[c] | Grassland[d] | Total |
| Rodentia | *Peromyscus maniculatus* | 153 | 231 (245)[e] | 59 (86) | 1 (2) | 444 |
| | *Microtus montanus* | 0 | 7 (7) | 330 (478) | 100 (171) | 437 |
| | *Perognathus parvus* | 206 | 72 (76) | 5 (7) | 0 | 283 |
| | *Eutamias minimus* | 101 | 159 (169) | 0 | 0 | 260 |
| | *Reithrodontomys megalotis* | 1 | 13 (14) | 36 (52) | 21 (36) | 71 |
| | *Dipodomys ordii* | 30 | 11 (12) | 0 | 0 | 41 |
| | *Dipodomys microps* | 9 | 2 (2) | 0 | 0 | 11 |
| | *Onychomys leucogaster* | 7 | 0 | 0 | 0 | 7 |
| | *Microtus longicaudus* | 0 | 0 | 3 (4) | 0 | 3 |
| | *Microdipodops megacephalus* | 3 | 0 | 0 | 0 | 3 |
| | *Spermophilus townsendii* | 2 | 1 (1) | 0 | 0 | 3 |
| | *Neotoma lepida* | 2 | 0 | 0 | 0 | 2 |
| | *Thomomys talpoides* | 1 | 0 | 0 | 0 | 1 |
| Carnivora | *Mustela frenata* | 0 | 1 (1) | 2 (3) | 0 | 3 |
| Insectivora | *Sorex vagrans* | 0 | 0 | 10 (14) | 0 | 10 |
| Lagomorpha | *Sylvilagus nuttallii* | 1 | 0 | 0 | 0 | 1 |
| | TOTALS | 516 | 497 (528) | 445 (645) | 122 (209) | 1,580 |
| | $H^1$ (f) | 0.605 | 0.549 | 0.389 | 0.207 | |

[a] Involved 5 plots and 8,232 trap nights.
[b] Involved 5 plots and 7,742 trap nights.
[c] Involved 4 plots and 5,684 trap nights.
[d] Involved 4 plots and 4,802 trap nights.
[e] Because unequal effort was expended in each habitat type, numbers in parenthesis represent relative totals for animals captured in greasewood, marsh, and grassland habitats, based on a total effort comparable to that made in sagebrush areas.
[f] Calculated as $H' = 1/N(\log_{10} n! - \Sigma \log_{10} n_i!)$ according to Lloyd et al. 1968, for the rodent species in each community type.

a factor of 5 seasonally. In the greasewood areas, however, among-plot differences in the density of pocket mice differed by as much as a factor of about 7; there was an equivalent difference in density within plots (Table 2). Although densities were generally lower on the greasewood than the sagebrush plots ($t = 4.29$, $df = 37$, $P < 0.001$), in both habitat types peak numbers of pocket mice were trapped from late April to early June. The lowest population densities occurred from late June through mid-August. These fluctuations in population density were similar in both timing and magnitude to those of a population of *P. parvus* studied by O'Farrell et al. (1975) in shrub-steppe habitat in southeast Washington. Densities of pocket mice apparently increased on most plots in the fall. This was probably the result of increased activity as temperatures cooled.

*Reproduction.*— Male pocket mice were in breeding condition from early May until early August. Peak breeding activity probably occurred in early June, a period not adequately represented by trapping data. Males were believed to be reproductively active about a month before the females, based on the percentage in reproductive condition in May (56 percent of males, 8 percent of females). Pregnant females were trapped almost exclusively in June, although sample size was small ($n = 4$), and no reproductively active pocket mice were trapped after 29 August in either habitat type.

Juvenile pocket mice were trapped from early May to early September on plots in sagebrush areas, although the majority were found from June through August. In greasewood areas, juveniles were trapped only from June through August (Fig. 2). Recruitment of juveniles was greatest in both habitat types during July.

*Dispersion.*— The trap-revealed dispersion of pocket mice on all plots differed significantly from random, and a clumped distribution pattern was evident. On each of three plots where 60 or more capture records of pocket mice were obtained, a significant relationship was evident between pocket mouse distribution and cover density. Significantly fewer pocket mice than expected were trapped in quadrats with less than 40 percent cover, but more pocket mice than expected were trapped in quadrats with greater than 40 percent cover ($X^2 = 26.33$, $df = 8$, $P < 0.001$).

The preference of pocket mice for areas of relatively dense cover undoubtedly was a response to the interaction of several factors. Increased vegetation possibly reduced the rate of predation (Rosenzweig and Winakur 1969, Brown and Lieberman 1973) and increased forage availability (O'Farrell 1975). It also probably beneficially affected microhabitat evaporation rates, humidity, and air temperature (Beatley 1976).

*Habitat.*— Although vegetation was of obvious importance in the local distribution of pocket mice, the abundance of this species in

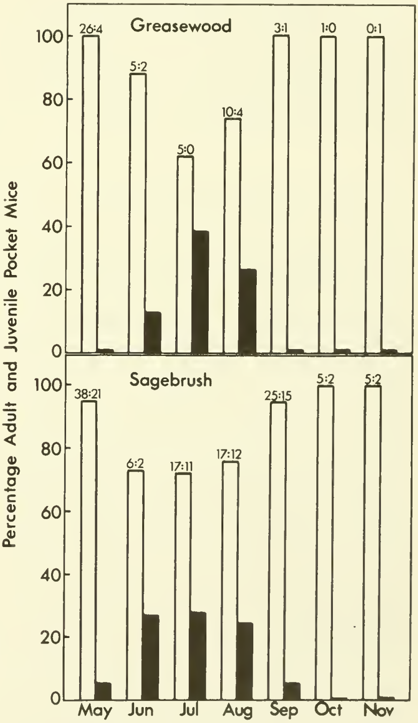

Fig. 2. Percentage of captures of pocket mice each month comprised of adult (open rectangles) and juvenile (solid rectangles) animals. Numbers atop open rectangles denote male:female sex ratios.

all sagebrush or greasewood areas was significantly correlated only with edaphic factors. A direct correlation between the population density of pocket mice and the percentage of sand on each plot was evident ($P<0.05$—Fig. 3A). The ability of pocket mice to dig through the surface layer of the soil is of obvious importance to their fossorial activities. The general importance of edaphic factors was further suggested by an inverse relationship between density and the percentage of clay in the soil ($P<0.05$—Fig. 3B). These factors probably affect burrow construction and stability. For example, soil texture has a direct influence on several aspects of soil moisture, including depth and rate of percolation, retention, and evaporation rates (Krynine 1947, Beatley 1976). In greasewood areas the mean soil moisture was inversely correlated with percentage of sand ($r^2=0.92$, $P<0.005$). However, Rosenzweig and Winakur (1969) found the distribution and abundance of five other species of pocket mice in Arizona showed no correlation with soil texture.

### *Eutamias minimus*

*Density.*— Least chipmunks also occurred only in sagebrush or greasewood communities. In the sagebrush community type, among-plot differences in the density of chipmunks generally were less than a factor of 3. Within-plot fluctuations in population density varied by an equivalent amount. In greasewood, among-plot variation in population density varied seasonally by a factor of about 6, with the exception of the 1973 trapping period. There was an equivalent variation within-plot seasonally (Table 2). In neither shrub community type was there a season during which peak numbers were evident. Vaughan (1974) also noted a fairly stable population density for this species in northern Colorado.

*Reproduction.*— Male chipmunks may have been reproductively active in both community types about one month before the females, as suggested by the percentage of each sex in breeding condition in May (91 percent of males, 40 percent of females). Breeding apparently was confined to a fairly brief period, with peak activity in late April and May. The number of chipmunks in breeding condition declined rapidly in both community types throughout the summer. No reproductively active chipmunks were trapped after 31 July in the greasewood areas or after 29 August in sagebrush areas. Davis (1939) and Gordon (1943) reported that this species mated from early to midspring in the northern part of its range, and Negus and Findley (1959) reported no sexually active least chipmunks occurring after late June in northwest Wyoming.

Of the 260 chipmunks captured during the study, only one was considered a juvenile. Juveniles were probably most numerous in early June, when no trapping was conducted. This is suggested by the reproductive data

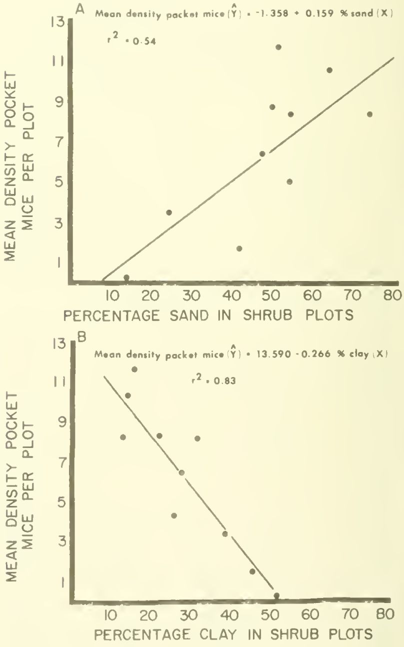

Fig. 3. Relationship between components of soil texture and mean density of pocket mice on 10 study plots in shrub communities on Malheur National Wildlife Refuge from July 1973 through June 1975. (A) Percentage of sand; (B) Percentage of clay.

above and the results of Hall (1946) and Linsdale (1938), who reported parturition in least chipmunks in Nevada occurred during May and early June. Tevis (1958) found gravid least chipmunks during mid-April in northeastern California. It is possible the age criteria may have been inadequate to distinguish juvenile chipmunks.

*Dispersion.*— On all plots where more than 23 capture records of chipmunks were obtained, their dispersion was clumped. On none of the plots was there a relationship between dispersion and the amount of vegetation cover. However, on only one plot were there as many as 60 location records.

*Habitat.*— On both shrub areas, the density of chipmunks was directly correlated with the mean depth of soil ($P < 0.05$, Fig. 4) and with soil strength ($P < 0.05$, Fig. 5). On sagebrush areas, a positive correlation was found between density and diversity of soil strength ($r^2 = 0.88$, $P < 0.01$). Correlations between the density of chipmunks and habitat factors on the greasewood areas included a direct relationship to the percentage of clay in the soil ($r^2 = 0.72$, $P < 0.05$).

As with pocket mice, the depth, texture, and strength of the soil would directly affect chipmunks in the construction and stability of burrows, and indirectly affect aspects of temperature and humidity. The densities of pocket mice and chipmunks were oppositely related to the percentage of clay in the soil; this suggests that chipmunks did not find it as difficult as the smaller pocket mice to dig through a sometimes hard, consolidated soil surface of high clay fraction.

### *Peromyscus maniculatus*

*Density.*— Deer mice exhibited the widest local distribution, being resident in sagebrush, greasewood, and marsh community types (Table 1). Deer mice generally were most abundant on the greasewood areas, where among-plot variation differed by a fac-

TABLE 2. Estimated population densities and standard deviation for four species of small mammals common on study plots (1.1 ha) in three community types on Malheur National Wildlife Refuge from July 1973 through June 1975.

| | | Sagebrush | | | | | | Greasewood | | | | | | Marsh | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *P. man.* | | *P. parvus* | | *E. min.* | | *P. man.* | | *P. parvus* | | *E. min.* | | *P. man.* | | *M. mont.* | |
| Period | Plot | N̄ ± | Sd | N̄ ± | Sd | N̄ ± | Sd | N̄ ± | Sd | N̄ ± | Sd | N̄ ± | Sd | N̄ ± | Sd | N̄ ± | Sd |
| 1973 July-Sept. | 1 | 4.8 | 0.4 | 5.5 | 0.9 | 7.7 | 3.2 | 9.3 | 2.0 | 8.7 | 2.7 | 1.7 | 0.7 | 5.6 | 0.9 | 0.0 | – |
| | 2 | 13.7 | 2.4 | 5.5 | 0.5 | 2.3 | 0.3 | 9.2 | 1.9 | 0.0 | – | 16.9 | 1.7 | b | | b | |
| | 3 | 2.3 | 0.3 | 8.4 | 0.4 | 2.0 | 0.6 | 6.2 | 1.2 | 0.7 | 0.7 | 6.5 | 2.6 | 0.0 | – | 169.5 | 30.0 |
| | 4 | 1.0 | 0.0 | 9.0 | 2.0 | 0.0 | – | 2.0 | 1.0 | 0.0 | – | 14.3 | 0.3 | 0.0 | | 252.8 | 82.2 |
| | 5 | 3.2 | 0.2 | 9.5 | 1.5 | 0.0 | – | 5.3 | 0.3 | 2.0 | – | 0.0 | – | – | – | –– | |
| 1974 June-Aug. | 1 | 2.8 | 0.4 | 9.3 | 0.9 | 7.9 | 1.1 | 6.5 | 0.9 | 8.3 | 0.9 | 2.1 | 0.7 | 5.2 | 1.0 | 0.0 | – |
| | 2 | 6.9 | 0.5 | 12.5 | 1.4 | 9.7 | 1.6 | 10.1 | 1.8 | 0.0 | – | 9.8 | 0.9 | 0.0 | – | 0.0 | – |
| | 3 | 0.8 | 0.3 | 5.8 | 0.8 | 3.6 | 0.4 | 9.1 | 0.7 | 1.3 | 0.2 | 10.7 | 1.6 | 4.7 | 0.8 | 46.6 | 5.4 |
| | 4 | 0.8 | 0.1 | 6.0 | 0.5 | 0.0 | – | 4.4 | 0.4 | 0.0 | – | 9.8 | 0.5 | 1.3 | 0.6 | 36.5 | 4.7 |
| | 5 | 2.9 | 0.1 | 4.4 | 0.7 | 0.0 | – | 4.4 | 0.5 | 4.0 | 0.3 | 0.0 | – | – | – | – | – |
| 1974 Sept.-Nov. | 1 | 6.3 | 0.5 | 15.1 | 2.6 | 6.4 | 0.6 | 7.2 | 0.4 | 11.9 | 0.8 | 5.1 | 0.8 | 8.2 | 1.1 | 0.0 | – |
| | 2 | 5.7 | 0.3 | 11.6 | 1.6 | 9.4 | 0.7 | 20.1 | 1.7 | 0.0 | – | 13.6 | 2.3 | 0.0 | – | 0.1 | – |
| | 3 | 3.0 | 0.0 | 5.4 | 0.2 | 5.9 | 0.7 | 17.0 | 1.0 | 1.8 | 0.2 | 6.6 | 0.8 | 6.4 | 0.5 | 33.9 | 6.7 |
| | 4 | 8.5 | 0.6 | 5.0 | 0.2 | 0.0 | – | 7.8 | 0.9 | 1.0 | – | 11.6 | 1.2 | 5.4 | 1.6 | 40.2 | 13.9 |
| | 5 | 24.4 | 0.4 | 6.7 | 0.3 | 0.0 | – | 4.3 | 0.9 | 0.7 | – | 0.0 | – | – | – | – | – |
| 1975 April-June | 1 | 0.8 | 0.1 | 10.8 | 0.9 | 13.9 | 1.0 | 3.5 | 0.5 | 3.4 | 0.3 | 5.9 | 0.7 | a | | a | |
| | 2 | 2.9 | 0.3 | 16.3 | 0.6 | 6.0 | 0.6 | a | | a | | a | | 0.0 | | 0.0 | |
| | 3 | 3.0 | 0.3 | 4.8 | 0.2 | 2.2 | 0.4 | 18.2 | 1.1 | 8.7 | 0.3 | 4.4 | 0.5 | 1.4 | 0.2 | 4.2 | 0.8 |
| | 4 | 14.8 | 0.8 | 12.0 | 0.8 | 0.0 | – | 15.0 | 0.9 | 3.9 | 0.8 | 3.5 | 0.4 | a | | a | |
| | 5 | 11.8 | 0.9 | 12.3 | 0.3 | 0.0 | – | 20.5 | 1.9 | 10.7 | 0.7 | 0.0 | – | – | – | – | – |

[a] Plot was flooded, could not be operated.

[b] Grid not operated during 1973.

tor greater than 3 only in 1973 (Table 2). Within-plot fluctuation in the density of deer mice also approached this magnitude. Populations of deer mice in sagebrush areas exhibited fluctuations in density comparable to those on greasewood areas. Both within- and among-plot variation generally differed by a factor of about 3. The densities of deer mice on sagebrush and marsh plots were about equal, with fluctuations in the marsh areas again relatively minor. There was no season during which the density of this species was

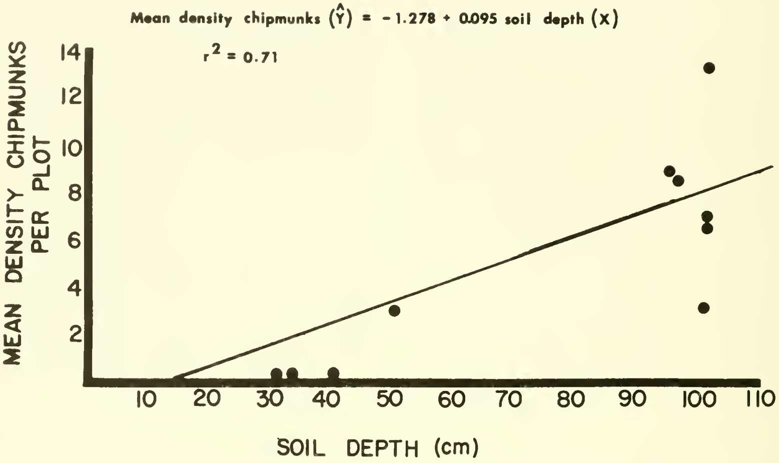

Fig. 4. Relationship between the density of chipmunks and soil depth on study plots in two shrub habitat types on Malheur National Wildlife Refuge from July 1973 through June 1975.

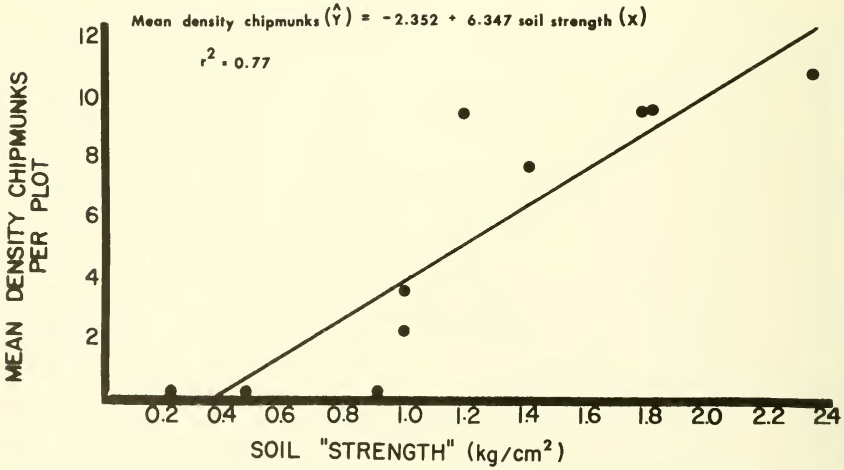

Fig. 5. Relationship between the density of chipmunks and soil "strength" on study plots in two shrub habitat types on Malheur National Wildlife Refuge from July 1973 through June 1975.

consistently highest, although density was generally lowest during the summer.

*Reproduction.*— Deer mice were reproductively active during all months that trapping was conducted, although a decline in breeding activity was evident during the summer. Parturition occurred at least as early as April in the shrub habitats, because juvenile animals were trapped in May (Fig. 6). Peak numbers of juveniles were on the plots in May and in the fall. It was not determined if breeding continued throughout the year, but, considering the usually harsh winter conditions on the study area, it seems doubtful. However, deer mice in sagebrush areas of east-central Washington have bred throughout the year (Scheffer 1924).

*Dispersion.*— The trap-revealed dispersion of deer mice in all habitat types differed significantly from random, and on 10 of 11 plots a clumped pattern was evident. Relationships between dispersion and cover in the marsh plots could not be evaluated because of too few captures in 1975. The results of this analysis on sagebrush and greasewood plots were equivocal. On greasewood plot 4 and sagebrush plot 5, significantly fewer deer mice than expected were captured in portions of those plots with less than 40 percent cover, but greater numbers than expected occurred in portions with more than 40 percent cover ($X^2 = 58.59$, df $= 8$, $P < 0.001$). However, on sagebrush plot 2 the opposite relationship was apparent ($X^2 = 7.53$, df $= 1$, $P < 0.01$), and on the remaining five plots, where sufficient capture records were available to allow analysis, there were no significant relationships between the amount of cover and the dispersion of deer mice.

These results reflect the range of relationships relative to cover previously reported for this species. A direct relationship between amount of cover and the local distribution and abundance of *Peromyscus* was described by Allred and Beck (1963). However, the proportion of cover did not exceed 25.0 percent in any of the areas sampled by these authors. An inverse relationship between cover and density was reported for several habitat types, including grassland and cultivated areas (Phillips 1936, LoBue and Darnell 1959, Tester and Marshall 1961), desert shrub (MacMillen 1964), and sites disturbed by strip-mining (Dusek and McCann 1975). In similar habitats, other researchers found no relationship between amount of cover and local distribution or abundance of deer mice (Rickard 1960, Verts 1957). It may be that no general relationship exists between the local distribution or abundance of deer mice and amount of cover.

*Habitat.*— There was a direct correlation between the density of deer mice and only one vegetative factor: the amount of vegetation at the three heights used to measure foliage height diversity. This correlation was evident on plots in both sagebrush areas ($r^2 = 0.98$, $P < 0.01$) and greasewood areas ($r^2 = 0.86$, $P < 0.25$). Thus, at least during the

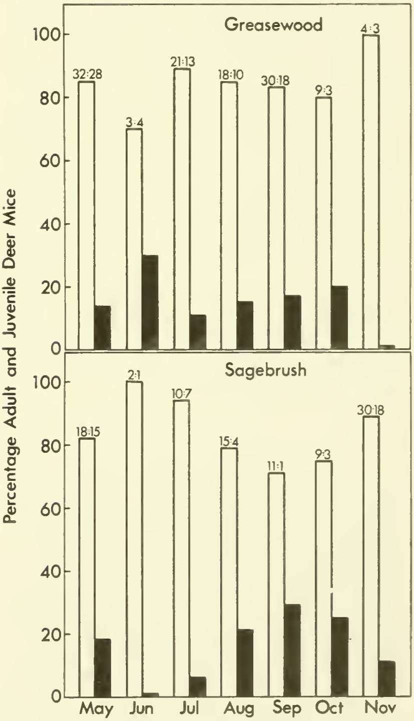

Fig. 6. Percentage of captures of deer mice each month comprised of adult (open rectangles) and juveniles (solid rectangles) animals. Numbers atop open rectangles denote male:female sex ratios.

summer, it appeared that deer mice in shrub communities selected for increased foliage, at least at the measured, interspersed levels of the vegetative profile, rather than a continuum of foliage above or below a particular height. Whether this relationship was of direct adaptive significance in predator avoidance, foraging or general scansorial tendencies (Horner 1954), or was indirectly associated with some other factor, was not readily apparent.

In marsh areas, a slight positive correlation existed between the density of deer mice and the percentage of sand in the soil ($r^2 = 0.37$, $P < 0.05$). On greasewood areas, an inverse relationship was evident between these two factors ($r^2 = 0.80$, $P < 0.025$), as well as a direct correlation between density of deer mice and the percentage of soil moisture ($r^2 = 0.30$, $P < 0.01$). Therefore, deer mice exhibited an opposite response to the percentage of sand on marsh and greasewood areas, and no relationship on sagebrush areas; habitats generally subjected to large differences in the amount of free water associated with them.

The permeability and drainage capabilities of soils vary directly with their percentage of sand (Krynine 1947). The opposite response of deer mice to the percentage of sand on marsh and greasewood plots may have resulted from an effort by deer mice to select an "optimal" moisture range within the continuum of soil moisture conditions that could be tolerated. That is, "wetter" arid areas and "drier" wet areas.

### *Microtus montanus*

*Density.*— In marsh areas, montane voles were resident only on plots 3 and 4, which were dominated by burreed (*Sparganium* sp.), as opposed to bulrush (*Scirpus paludosis*) and spikerush (*Eleocharis palustris*) on plots 1 and 2. The density of voles during 1973 was the highest of any small mammal during the study. Densities declined sharply after the initial trapping period. In 1975, the population density of voles on marsh plot 3 was reduced from the 1973 estimate by a factor of at least 20 (Table 2). Although the population densities of voles in grassland areas were generally lower than in marsh areas, the grassland plots were continuously altered by land-use practices throughout the field work, and trends in the density of voles were difficult to determine.

*Reproduction.*— The reproductive data for voles were not as complete as those for other species of small mammals. Reproductively active voles were trapped in marsh areas only from July through September. However, montane voles were undoubtedly breeding during the spring months (Bailey 1936), when trapping was not conducted in marsh or grassland communities. Also, considering the short gestation period of this species (Asdell 1964), and that juvenile voles were trapped in early November, breeding must also have occurred in October. There was no period during which the juvenile increment of the population or the percentage of adults in breeding condition was consistently largest.

*Dispersion.*— The trap-revealed dispersion of voles on all plots differed significantly from random, and a clumped pattern was evident. On the only plot where the analysis could be made, the dispersion of voles was related to the amount of cover. Voles were trapped significantly more often in quadrats where cover was greater than 80 percent ($X^2 = 15.49$, $df = 1$, $P < 0.005$).

*Habitat.*— There was a weak, direct correlation between the estimated population densities of voles and the mean amount of cover on plots in marsh ($r^2 = 0.41$, $P < 0.01$) and grassland communities ($r^2 = 0.41$, $P < 0.025$). In a related manner, an inverse relationship was evident between the density of voles and the patchiness of cover of these habitat types ($r^2 = 0.41$, $P < 0.01$ and $r^2 = 0.64$, $P < 0.01$, respectively). The direct relationship between the occurrence of *M. montanus* and dense cover is well documented (Bailey 1936, Hodgson 1972), and, as Getz (1961) discussed, it is difficult to separate the relative functions of cover, and importance to montane voles, in terms of protection from predators, microhabitat modification, and food resources. That cover is important to this species was further shown by a comparison of vole densities on grassland plots 3 and 4, sampled concurrently in August and November 1974. In August there was no statistical difference in estimated vole densities on each plot (19.1 and 15.4, respectively). Plot 3 was undisturbed prior to the second trapping period and the density of voles was unchanged (20.3 per plot). However, plot 4 was mowed two months prior to the second trapping period, and only one individual was caught in November. A similar effect was reported by LoBue and Darnell (1959) for a harvested alfalfa field. No other vegetative or edaphic factor was related with the density of montane voles.

### General Vegetative Structure

When each of the four habitat types investigated was viewed in terms of their general physiognomy (Elton and Miller 1954), essentially two structural types were evident, each with a characteristic small mammal fauna. One type consisted of the 10 plots in the sagebrush or greasewood shrub vegetation. This type had relatively few plant species but a relatively large degree of structural diversity. The other physiognomic type, which consisted of the eight plots in marsh or grassland areas, was characterized by a large number of plant species, at least in grassland areas, but a generally low degree of structural diversity.

With the exception of deer mice, each species of small mammal was restricted to one of the two physiognomic types. The small mammal fauna associated with the sagebrush-greasewood type was relatively diverse. It included the four species of heteromyids captured, the only species of chipmunk found on the refuge, and five other rodent species (Table 1). Voles, western harvest mice (*Reithrodontomys megalotis*), and shrews (*Sorex vagrans*) were restricted to the marsh-grassland physiognomic type. Although the small mammal fauna was not as diverse, large population densities were encountered in this type. It should be noted that voles and harvest mice were not considered residents in greasewood areas. The only individuals of these species captured in greasewood habitat were found on plot 5. These 20 individuals were captured while a fire smouldered in dry marsh vegetation 40 m from the plot during September 1974. Presumably, these conditions forced voles and harvest mice from their preferred habitat, as neither of these species were captured on plot 5 during the two trapping periods prior to the fire. Dice (1931) first suggested that the physiognomy of the vegetation was an important factor in the local distribution of animal species. Since then, this generalization has been corroborated with regard to many species of small mammals (Hardy 1945, Fautin 1946, Pearson 1959, Tester and Marshall 1961, M'Closkey and Lajoie 1975); and the effect of foliage structure on the distribution of species of small mammals was evident in this study.

## ACKNOWLEDGMENTS

I thank Dr. B. J. Verts, Department of Fisheries and Wildlife, Oregon State University, for valuable assistance during all phases of this work. Personnel of Malheur National Wildlife Refuge provided lodging, transportation, and other assistance while in the field. Several figures were provided by the Appalachian Environmental Laboratory, Center for Environmental and Estuarine Studies, University of Maryland. This is a technical paper from the Oregon Agricultural Experiment Station, Corvallis, Oregon, 97331, Contribution No. 950, Appalachian Environmental Laboratory, Center for Environmental and Estuarine Studies, University of Maryland.

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# INFLUENCE OF PRECIPITATION AND TEMPERATURE ON RING, ANNUAL BRANCH INCREMENT, AND NEEDLE GROWTH OF WHITE FIR AND DOUGLAS-FIR IN CENTRAL UTAH

John D. Shane[1,2] and Kimball T. Harper[1]

Abstract.— The study evaluates growth variations in mixed stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and White Fir (*Abies concolor* Hoopes) from the Bighorn Ranch in northern Sanpete County, Utah. The study area lies 26 km southwest of Thistle, Utah. Tree-ring width, annual branch growth and needle length for the period 1970–1976 were obtained from Douglas-Fir and White Fir individuals distributed along an altitidinal and moisture gradient. Elevation ranged from 2257 m to 2500 m above sea level.

Temperature and precipitation are shown to exert a significant influence on needle and annual branch growth and width of the annual rings. It was found that multiple correlation coefficients were always larger than the simple correlation coefficients. This suggests that the trees are responding to both temperature and precipitation. Annual branch growth is shown to be positively correlated with ring width and needle length. The influence of precipitation on growth is synchronized with 1 October–1 June precipitation. Best growth occurs in cool, moist years and at lower elevations.

Work on growth variations in conifer trees is not new. The use of ring width as a relative measure of secondary growth has long been studied in the West and Southwest (Douglass 1919, Fritts et al. 1965, Fritts 1966, Tappeiner 1969, Kozlowzki 1971, Drew 1972). The fact that variations in ring width sequences from certain trees may be used to date wood (Douglass 1919) and reconstruct past climates (Fritts 1971, Stokes and Smiley 1968, Arnold 1947, Chaloner and Creber 1973, Seward 1892, Schwarzbach 1971, Antevs 1953) is well established. There is, however, a paucity of research on normal variations in needle retention and length as well as annual branch growth for these conifer trees, although some research has been done (Lamb 1969, Peckham 1973). Such research is needed to detect the effects of low levels of atmospheric contaminants on tree growth. Research has demonstrated that air pollution can induce abnormal, nonclimatic variation in ring width and needle length and retention. Pollutants can depress width of tree-rings (Nash et al. 1967) and needle length and vigor (Anderson 1966, Teshow 1968, Treshow et al. 1967). Although Nash et al. (1975) could not directly link air pollution with decreased ring width, it was strongly implicated. Reduced needle length and vigor have been directly linked to air pollutants of various kinds, as shown by Treshow et al. (1967), Treshow (1968), and Anderson (1966). An extensive bibliography and discussion of air pollution and its affects on trees can be found in Mansfield (1976). The effects of air pollution from fluoride, dust, or sulphur dioxide were considered to be negligible in this study, largely on the basis of the general vigor of Douglas-fir, which is considered to be the most susceptible of all the western trees to the pollutants listed (Anderson 1966).

The interpretation of variations in tree growth requires a constant appreciation of the fact that a living tree responds to many external and internal factors. Fortunately for the analyst, only a few of the environmental factors may exert a major influence on growth. The more pronounced variations in growth may thus be attributable to only one or two factors. Therefore, as Lyon (1936:457) states, "the practical approach to the problem is to notice the responses to extreme values of the factor suspected of being outstanding in its control of growth rate."

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Growth control may be either direct or indirect or both. However, it is not known how many of these effects are caused directly or indirectly (Kramer 1964). Many interrelated factors (such as temperature, light, evaporation, interception of precipitation by the tree crown, cone production, root distribution, etc.) influence growth. Failure to allow for such contribution factors could lead to erroneous correlations or to none at all.

Finally, it should be pointed out that correlations established between variables over a long period of time are probably more significant than those over relatively short periods of time. The foregoing statement has special relevance when an ephemeral property such as needle length is correlated with annual branch increment or annual ring width. Therefore, a close inspection of needles should be made from year to year and the appropriate data taken. For example, years with heavy cone production show significantly reduced annual ring increment and shoot and needle elongation, even though precipitation is held constant (Tappeiner 1969).

## METHODS

One mixed stand of Douglas-fir and White Fir was chosen at 2257 m and another at 2500 m. Five trees of each species were sampled at the lower elevation stand and six trees of each species were sampled at the higher elevation site. Sampled trees were healthy, mature individuals. Branches were taken from a height of 1.5–2.5 m above ground on trees sufficiently isolated from one another to receive full light on all sides. Sampled branches were not consistently taken from a given side (i.e., north, south, east, or west) of trees, because Peckham (1973) has shown that leaf parameters for these species do not differ significantly from one side to another on open grown trees.

Ring width samples were taken from cores removed from sample trees with a Swedish increment borer. The cores were taken approximately 1.0 m from the ground. Growth ceases at the base of the tree before it ceases toward the crown (Kramer 1964); thus, the base of the tree will record significant changes in precipitation and provide the most accurate record of macroclimatic variation (Fritts 1966).

Precipitation and temperature data (Table 1) for the period 1 October–30 June of each year of concern were obtained from Utah Climatological Data (1969–1976) for the Santaquin Power House Station some 33 km to the northwest of the study area. The number of days below 0 C for the period March through June were obtained from the Moroni weather station 33 km to the south of the study area (Table 2). Trials demonstrated that Santaquin precipitation and temperature data correlated better with all tree growth parameters than comparable data from Moroni (and better than the average for Santaquin and Moroni precipitation and temperature data). Conversely, Moroni data for days below 0 C correlated better with true growth than similar data from Santaquin. Precipitation and temperature for the period October–December of the preceding year and January–June of the tree growth year under consideration were used for correlation analyses aimed at determining the impact of precipitation on the several measures of tree

TABLE 1. Temperature and precipitation data for the study area at the Santaquin Power House Station during the years 1970–1976.

| Year | Average October–June temperature (degrees C) | Average October–June precipitation (cm) |
|---|---|---|
| 1970 | 6.3 | 37.0 |
| 1971 | 6.3 | 33.9 |
| 1972 | 7.1 | 33.0 |
| 1973 | 5.4 | 54.5 |
| 1974 | 7.2 | 30.1 |
| 1975 | 4.9 | 37.2 |
| 1976 | 5.9 | 30.6 |

TABLE 2. Number of days below 0 C at Moroni for the period March 1–June 30.

| Year | Total |
|---|---|
| 1970 | 65 |
| 1971 | 56 |
| 1972 | 54 |
| 1973 | 66 |
| 1974 | 53 |
| 1975 | 63 |
| 1976 | 60 |

growth (e.g., 1970 growth variables were paired with October–December 1969 plus January–June 1970 precipitation). Average needle length, average branch length, and average growth ring increment for each year were thus correlated with precipitation and temperature data for that year (offset from calendar year as indicated above). Average needle length was obtained by measuring needles from the beginning, middle, and end of the year's growth on each branch and is reported to the nearest .5 mm, using a Wilde dissection microscope and a millimeter ruler. The annual branch growth was measured between successive terminal bud scars. Average needle retention for each species was also taken.

## Results and Discussion

The growth of Douglas-fir and White Fir differed significantly from year to year between elevations. The greatest average needle growth for Douglas-fir and White Fir was in 1973 at both higher and lower elevations (Tables 3 and 4). This correlates nicely with the fact that the average annual precipitation during the period of record (1970–1976) was highest in 1973. The heavy precipitation of 1973 was associated with normal annual temperature. It is significant that ring width and branch length were also maximal in 1973 for both elevations and species. Radial increases and elongation are directly linked to foliage development (Larson 1964 and Tables 5 and 6).

Average needle length for both Douglas-fir and White Fir were greatest at the lower elevations (Tables 3 and 4). This seems to be in direct contrast to what Peckham (1973) described for Douglas-fir. He found that needle length was greatest at the higher elevations with one exception, although he doesn't elaborate on this exception. Peckham's (1973) findings are reconcilable if one considers that the trees at the lower elevation were experiencing a cold air runoff effect from the higher elevations. However, there are other factors which could effectively bring about the reverse situation of having the longer needles at the lower elevations. These factors might be prolonged snow pack at the higher elevations that might allow the lower elevation trees to get a head start in the growing season.

To examine the effects of temperature on the trees, the number of days during the critical growing season at or below 0 C was measured (Table 2). It appears that freezing temperatures have little discernible effect on annual increment, annual branch length, or needle length (Tables 7 and 8). The possible exception to this might be the year 1975. In that year there was an abnormally large number of days below freezing in the month of May. These freezing temperatures can be implicated in a stunting of the apical meristems and a retardation of growth in 1976. There may have been an integrated effect of climate on food making and food accumulation throughout the 14 to 15 months previous to and including the 1976 period of growth. Therefore, a bad year may exert its effects on the subsequent year's growth (Fritts et al. 1965, Peckham 1973).

The effects of precipitation on the growth rings and branch lengths is indirect (Larson 1964). The needle lengths are directly affected by the amount of moisture and they control the auxins necessary for cambial activity.

Table 3. Douglas-fir Measurements at 2257 m above sea level (top) and at 2500 m above sea level (below). Each value is an average based upon five trees at the lower elevation and six trees at the higher elevation.

| Year | Ring width increment (mm) | Annual branch growth (mm) | Needle length (mm) |
|---|---|---|---|
| 1970 | 2.9 | 48.0 | 26.8 |
| 1971 | 2.9 | 69.5 | 35.0 |
| 1972 | 2.6 | 55.1 | 29.6 |
| 1973 | 4.3 | 68.3 | 35.9 |
| 1974 | 2.5 | 41.1 | 28.4 |
| 1975 | 3.6 | 70.0 | 29.8 |
| 1976 | 2.7 | 44.6 | 31.5 |

| Year | Ring width increment (mm) | Annual branch growth (mm) | Needle length (mm) |
|---|---|---|---|
| 1970 | 1.8 | 38.1 | 30.0 |
| 1971 | 1.8 | 43.8 | 29.8 |
| 1972 | 1.8 | 37.6 | 27.7 |
| 1973 | 2.3 | 46.0 | 29.7 |
| 1974 | 1.5 | 36.6 | 23.9 |
| 1975 | 2.3 | 42.0 | 29.1 |
| 1976 | 1.3 | 36.6 | 27.5 |

Thus, the indirect effect is transmitted via the phloem. However, as previously noted, there is a depletion effect of the hormones the further down the stem one goes. Therefore, one might expect a comparatively less pronounced effect of precipitation in the annual increment than in the annual branch length of the branches. This is demonstrated to be the case. In dry seasons wood formation usually stops quite early in the summer because of water stress, but in wet seasons it may continue until September or October and finally is slowed down and stopped by the processes associated with low temperatures and decreasing photoperiod (Kramer 1964). This fact correlates nicely with growth throughout the tree (Tables 3 and 4).

Correlation among growth variables for both White Fir and Douglas-fir for both elevations are shown in Tables 5 and 6. All growth variables for both species are positively correlated among themselves, but the interrelationships are usually not statistically significant. Thus prediction of one growth variable from another would be risky. Each growth response apparently has a unique relationship to environment. The simple correlations for each growth variable on each environmental variable are reported in Table 7. All growth variables are positively correlated with precipitation, but temperature and days below 0 C usually negatively affected all the growth parameters that were considered.

Multiple correlation coefficients are always larger than any simple correlation coefficient for the relationship between a particular growth parameter and the environment variables considered (Tables 7 and 8). That result strongly suggests that more than one environmental factor has a significant impact on growth. In stepwise multiple regression analyses (Table 8), precipitation usually enters the analysis first; temperature usually follows precipitation in order of entry into the analysis, but its contribution to the ($R^2$) is generally small. Days below 0 C have their greatest impact on needle length, but even there the impact is weak.

Needle retention data have been reported for Douglas-fir and White Fir. Peckham (1973) reports needle retention in Douglas-fir of 3 or 4 to more than 20 years. Lamb (1969)

TABLE 4. White Fir measurements at 2257 m above sea level (top) and at 2500 m above sea level (below). All values are based on five trees at 2257 m and six trees at 2500 m elevation.

| Year | Ring width increment (mm) | Annual branch growth (mm) | Needle length (mm) |
|---|---|---|---|
| 1970 | 2.7 | 44.7 | 33.0 |
| 1971 | 3.4 | 51.0 | 35.0 |
| 1972 | 2.4 | 36.6 | 35.5 |
| 1973 | 3.3 | 56.7 | 38.3 |
| 1974 | 2.3 | 36.7 | 28.3 |
| 1975 | 3.2 | 48.4 | 34.9 |
| 1976 | 2.5 | 35.1 | 27.8 |

| Year | Ring width increment (mm) | Annual branch growth (mm) | Needle length (mm) |
|---|---|---|---|
| 1970 | 1.3 | 45.3 | 29.0 |
| 1971 | 1.9 | 44.2 | 34.0 |
| 1972 | 1.4 | 44.5 | 28.4 |
| 1973 | 2.2 | 49.1 | 33.6 |
| 1974 | 1.1 | 39.2 | 28.6 |
| 1975 | 1.8 | 39.7 | 31.8 |
| 1976 | 1.1 | 35.7 | 25.7 |

TABLE 5. Correlation among growth variables at 2257 m.

| Variables compared | Correlation coefficient (r) | |
|---|---|---|
| | Douglar-fir | White Fir |
| Ring width-needle length | .54 | .69 |
| Ring width-annual branch growth | .71 | .96++ |
| Needle length-annual branch growth | .66 | .78+ |

+ = significance at the .05 level
+ + = significance at the .01 level

TABLE 6. Correlation among growth variables at 2500 m.

| Variables compared | Correlation coefficient (r) | |
|---|---|---|
| | Douglar-fir | White Fir |
| Ring width-needle length | .58 | .93++ |
| Ring width-annual branch growth | .79+ | .66 |
| Needle length-annual branch growth | .64 | .64 |

+ = significance at the .05 level
+ + = significance at the .01 level

reports needle retention in White Fir to be from 12 to 20 years. There was no significant trend in years of retention at varying elevations in either study. Table 9 shows needle retention for Douglas-fir and White Fir. Our data show Douglas-fir to retain needles about 9 years at low elevations and 6 years at higher elevations. White fir holds needles 8–9 years at both elevations.

Considering all the above data, it is difficult to say which of the trees is responding more closely to the environment and at what elevation. White Fir has a range in elevation between 1833–3850 m and Douglas-fir grows from sea level to timberline (Cronquist et al. 1972). Needle retention for White Fir is greater than for Douglas-fir at 2500 m; the situation is reversed at 2257 m (Table 5). Although the sample size is somewhat less than one needs to draw conclusions, the results may indicate that White Fir is better adapted at the higher elevation in our study area.

Douglas-fir and White Fir at both elevations are very similar with respect to annual ring width increment and needle length. However, there is great disparity in the lengths of the branches between the two species. At 2257 m the branches on Douglas-fir are visibly longer than those on White Fir, and at 2500 m White Fir has the longer branches (Tables 3–4). There seems to be a similar trend here (as in needle retention) for White Fir to respond more favorably then Douglas-fir at the higher elevation, but for Douglas-fir to respond more favorably at the lower elevation.

## CONCLUSIONS

Environment plays a decisive role in tree growth through its effect on annual increment, annual branch length, and needle length. Nevertheless, the effect of the environment is considered to be primarily indirect. Environment induces either temporary fluctuations or long-term modifications on growth.

Considerable annual variation occurred in needle length and branch length and to a lesser degree in annual ring width increment. Optimum growth for the above three criteria is shown to be related to elevation and annual precipitation.

The data contained in this report will be useful in determining normal macroenvironmental growth patterns and variations for the tree species studied. This information would be useful in determining the local effects of air pollutants and/or climatic variations in the future.

One of the purposes of this study was to test an in-the-field method for determining year-to-year growth variation for two conifer tree species. It is our opinion that this type of evaluation could be done most accurately by inspection of the annual ring width increment and secondarily with annual branch lengths. The field observer is also encouraged to pay close attention to cone production of the trees, as it will have a marked effect on all aspects of growth.

We suggest that White Fir and Douglas-fir respond differently to environment as modi-

TABLE 7. Correlations between various independent and dependent variables for Douglas fir and White Fir at two elevations.

| | Douglas-fir | | | White Fir | | |
|---|---|---|---|---|---|---|
| Independent variables | Ring width | Branch growth | Needle length | Ring width | Branch growth | Needle length |
| | | | Elevation 2257 m | | | |
| | | | Simple correlation coefficient | | | |
| Precipitation (log) | .94$^{++}$ | .60 | .52 | .63 | .83+ | 77+ |
| Temperature | −.79$^{+}$ | −.63 | −.38 | −.70 | −.63 | −.38 |
| Days below 0 C | −.23 | −.01 | −.17 | −.36 | −.33 | .33 |
| | | | Elevation 2500 m | | | |
| Precipitation (log) | .80$^{+}$ | .79$^{+}$ | .58 | .80 | .75$^{+}$ | .64 |
| Temperature | −.64 | −.61 | −.60 | −.60 | −.03 | −.42 |
| Days below 0 C | .05 | −.24 | −.02 | −.09 | +.25 | −.23 |

$^{+}$ = significance at the .05 level
$^{++}$ = significance at the .01 level

TABLE 8. Stepwise multiple regression results for the effects of October–June precipitation, average October–June temperature, and days below 0 C for the period March–June on three growth parameters. Results are given for Douglas-fir and White Fir at two elevations.

Elevation 2257 m

| Independent variable | Douglar-fir | White Fir |
|---|---|---|
| **Ring width** | | |
| | Contributions to $R^2$ | |
| Precipitation (log) | .88 | .08 |
| Temperature | .09 | .49 |
| Days below 0 C | .00 | .02 |
| Total $R^2$ | .97 + + | .59 |
| **Branch length** | | |
| Precipitation (log) | .08 | .69 |
| Temperature | .40 | .01 |
| Days below 0 C | .05 | .07 |
| Total $R^2$ | .53 | .77 |
| **Needle length** | | |
| Precipitation (log) | .27 | .59 |
| Temperature | .00 | .01 |
| Days below 0 C | .02 | .15 |
| Total $R^2$ | .29 | .75 |

Elevation 2500 m

| Independent variable | Douglar-fir | White Fir |
|---|---|---|
| Precipitation (log) | .64 | .65 |
| Temperature | .05 | .03 |
| Days below 0 C | .05 | .00 |
| Total $R^2$ | .74 | .68 |
| **Branch length** | | |
| Precipitation (log) | .62 | .57 |
| Temperature | .04 | .24 |
| Days below 0 C | .01 | .01 |
| Total $R^2$ | .67 | .82 |
| **Needle length** | | |
| Precipitation (log) | .41 | .08 |
| Temperature | .00 | .36 |
| Days below 0 C | .03 | .04 |
| Total $R^2$ | .44 | .48 |

+ + = significance at the .01 level

TABLE 9. Needle retention by altitude for:

Douglas-fir

| Altitude (m) | Sample size | Years of needle retention |
|---|---|---|
| 2257 | 138 | 9.2 |
| 2500 | 102 | 5.7 |

White Fir

| Altitude (m) | Sample size | Years of needle retention |
|---|---|---|
| 2257 | 123 | 8.2 |
| 2500 | 159 | 8.8 |

fied by elevation in respect to annual ring width increment and branch lengths.

## ACKNOWLEDGMENTS

The authors gratefully acknowledge the critical discussions of Prof. Glen Moore (Brigham Young University) and the help of Mrs. Terris Shane for preparation of the early stages of this manuscript.

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# STUDIES IN NEARCTIC DESERT SAND DUNE ORTHOPTERA, PART XVI: A NEW BLACK *STENOPELMATUS* FROM THE MESCALERO SANDS

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Abstract.— *Stenopelmatus mescaleroensis* is described from New Mexico as new to science. A key to the *Stenopelmatus* of the United States is presented with notes on chaetotaxy used for these crickets.

In 1959, while studying the environmental relationships of sand dune biotae, one of my study areas was the Mescalero Sands, 45 miles east of Roswell, New Mexico. This extensive sand area, covered with scrubby oak, is one of many in the Pecos Desert, most northern of three eremological components of the Great Chihuahuan Desert. On the night of 6–7 July and on the night of 12–13 September, 1959, I took a black Jerusalem Cricket on each of those nights. Again, the evening of 6 September 1978, as the sun was setting, I collected 6 additional specimens, most of which were crawling actively across the dune blowouts surrounded by scrub oak. Before describing this species I wish to comment on the chaetotaxy of stenopelmatid crickets.

Because considerable confusion has existed concerning definition in the chaetotaxy of these orthopterans, I wish to define and unify ideas about their leg spination. Spines are usually small to large, solid, immovable projections, acuminate in form, such as those found along both external and internal dorsal margins of the methathoracic tibiae. In the past these have often been referred to as teeth. Spurs, on the other hand, have movable bases, and like the spines are small to large and acuminate or aciculate in form. Calcars are those very large spurs situated at the apices of all tibiae, and these are of considerable value in taxonomy, because in some species the posterior apical face is sometimes truncate and spathulately enlarged for digging or pushing in the sand or soil. In *Ammopelmatus* and *Viscainopelmatus*, these calcars are very short, even, and spathulately enlarged for sand propulsion. Whether the basal dorsal spines of the caudal tibiae are smaller or larger than those more apical spines is also of key importance.

### *Stenopelmatus mescaleroensis*, n. sp.

Description: This species differs from all American species of the genus by being totally black, although most Mexican species are black but not here considered. Size large to very large with some megacephalism present, although whether this feature is a sign of maturity in males is not clearly understood. Coloration in all other large American species of *Stenopelmatus* reddish orange to orange (desert) with much black on abdominal tergites; in smaller species such as *pictus* Scudder and *nigrocapitatus* Tinkham & Rentz, usually with shining black on head and parts of pronotum. Pronotum typical, foremargin almost squarely truncate, prozonal area broader than metazonal area so that lateral margin of prozona considerably constricted into lateral margin of the metazona, which posteriorly is very broad rounded into short truncate posterior margin. Abdomen typical of genus. Head broader than prozona of pronotum; very tumid and rounded, thus indicating some megacephalism. Antennae typical.

Leg spination as follows: Cephalic legs: dorsal line of femora very strongly arcuate, lower margin almost straight; dorsal margin

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of tibiae slightly sinuate in basal third, ventral margin rounding (not keeled) and moderately arcuate with four calcars, the three most apical largest (central largest) and the fourth a short pointed calcar situated on external margin. Dorsal margin in extreme subapical position bearing a spur as large as two that flank central and largest of three apical calcars. On ventral margin are two uneven subapical spurs and one small spur located about apical third immediately basad of most posterior of two uneven subapical spurs. Cephalic tarsus with first segment about equal to fourth, which bears claws or ungues, and almost twice length of short second and third segments; long protarsal first segment possibly composed of two fused segments.

Mesofemora much more slender than profemora; dorsal margin less strongly arcuate, lower margin almost straight. Mesotibiae

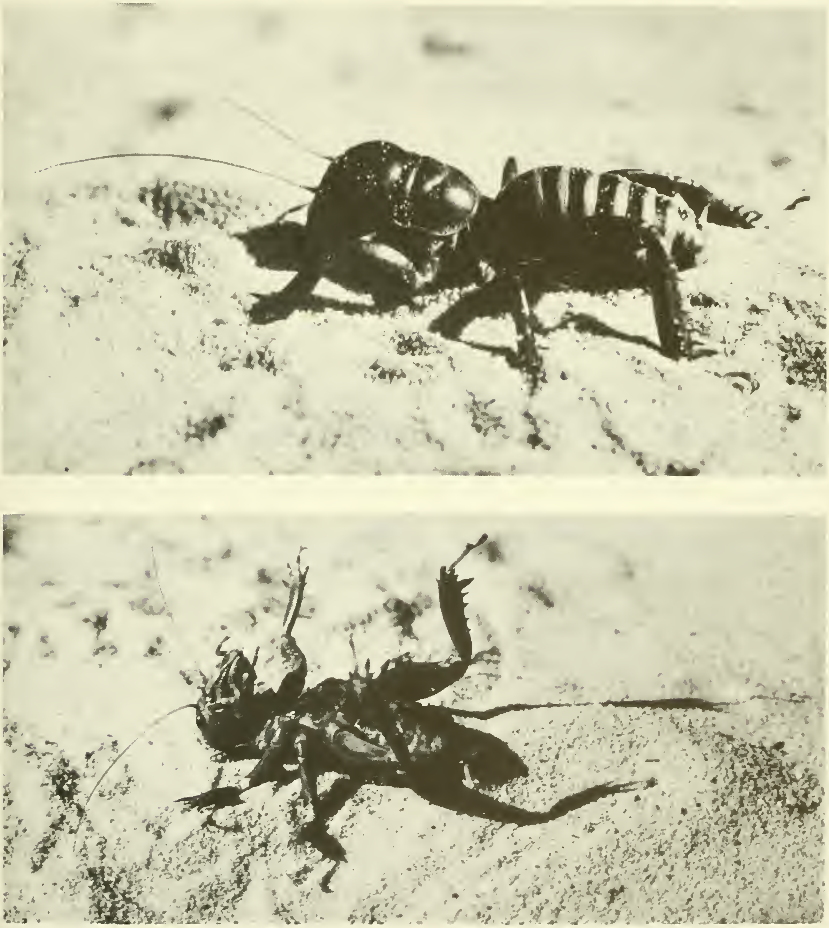

Fig. 1. *Stenopelmatus mescaleroensis* male holotype above; aggressive position below.

slightly less slender than protibiae, with four more evenly placed calcars apically and ventral margin (upper in folded leg) bearing a pair of appressed, short, acuminate spurs in extreme subapical position and dorsal margin (ventral in folded leg) bearing four strong acuminate spurs, two exterior placed about centrally and one in apical four-fifths; two internal at about apical third and basal one-third. Middle tarsus much as in cephalic tarsus with strong evidence of a central constriction in first long mesotarsal segment, thus indicating fusion of two segments.

Caudal legs: Caudal femora with dorsal margin strongly arcuate in lateral profile and rounded (not keeled); ventral margin relatively straight with founded inner and outer keels. Caudal tibiae heavily constructed with ventral margin (dorsal in folded legs) arcuate with one pair of large, appressed, acuminate spurs just basad of two large central calcars; dorsal margin (ventral in folded legs) straight and bearing 3 external spines in apical half and increasing in size apically, largest and most apical with posterior distal portion truncate and slightly spathulate, internal margin bearing 5 strong spines from near base to apex, all increasing in size distally, most apical, largest, with its apical posterior face truncate. Protarsi with first segment half length of entire tarsus, with strong evidence that first segment is composed of two fused segments.

Abdomen: with a pair of black uncinate hooks just interad of bases of white, hairy, erect cerci; this feature taken as proof of maturity of male specimen.

Measurements in millimeters by calliper: Type male, Mescalero Sands, 45 miles E Roswell, New Mexico, 6 Sept 1978, 7 p.m. E. R. Tinkham. Body length 38.5 mm; head breadth 11.2, depth (vertex to base of labrum) 14.0. Pronotum: prozonal width 12.1; metazonal width 11.4, length 8.5 mm. Abdominal length 24.0. Caudal femora 12 × 4.8; caudal tibiae 13.1 mm. Type in the Tinkham Eremological Collection. Paratypes: 7 males from the identical location on the extensive Mescalero Sands, all by me; two males by Mr. Jacques Helfer believed to be from the same location. One male, night of 6–7 July 1959 (after dark); one male, night of 11–12 September 1959, shortly after dark; 5 males, 6 September 1978, last two hours of setting sun; Helfer males, 1 September 1961, very well preserved by stuffing abdomen with cotton and pinning. It is interesting and unusual to have ten males and not a single female or immature to be represented in the collections. Range in measurements of paratype males: Body length 27.5–36.5 mm; head breadth 8.8–11.5 × depth 9.0–12.0 mm. Pronotum: prozonal width 8.8–12.3; metazonal width 7.8–10.3; pronotal length 6.0–8.0 mm. Caudal femora 9.9–12.3 × 3.9–5.0; caudal tibiae 9.0–12.5; abdomen 16.2–19.6; antennae 16.5–19.5 mm. Paratypes, other than size range, identical to the holotype in every respect.

Habitat: Scrub oak covered by drift-sand in areas with numerous cup-shaped depressions formed by the dune blowouts, their margins usually lined with scrub oak or a great variety of other plants, including different species of tall grass. In places there are ridges of drift sand frequented by a species of sand-treader (*Ammobaenetes*) in the spring and early summer as well as one very large area of open sand inhabited by a small herd of prong-horned antelope (as of 1959).

Flora: The Mescalero Sands have a large floral list the dunes and drift sand areas are covered with a scrubby growth of Harvard oak (*Quercus harvardii*), plus many other shrubs such as silver sage (*Artemisia filiformis*), mesquite (*Prosopis juliflora*). Bear Grass (*Yucca elata*), the delicate blue-flowered *Commelina communis*, the fragrant snowball flower (*Abronia fragrans*), the white-flowered *Solanum alba*, plus *Asclepias, Gilia, Oenothera, Cryptantha*, composites, cacti, and many grasses.

Orthopteran associates: In the fall and probably in the spring, as my fall collecting shows, this new black Jerusalem Cricket is active in the setting sun when it crawls rapidly across the large sandy blowouts. Orthopterans at this time include such acridids as *Trimerotropis citrina neomexicana* (the type locality; fairly common), the rarer *T. pallidipennis salina*, the rare *Spharagemon collare cristatum*, the very abundant *Schistocerca alutacea* and *Melanoplus glaucipes*, the slant-faced *Eremiacris virgata*, as well as a great number of other acridids, stick insects, and mantids. In the early summer *Xanthippus* *montanus* and *X. corallipes*, *Mestobregma* and *Arphia*, as well as many more are present. Nocturnal associates include: *Rehnia cerberus*, *R. (Neobarretia) victoriae*, *Pediodectes stevensoni* and *daedalus*, leaf katydids such as *Amblycorpha huasteca*, *Scudderis* spp., and many others as well as crickets. The small sand treader *Ammobaenetes* sp. on the sand ridges in the spring and summer undoubtedly is associated with the new *Stenopelmatus*. In fact, the Orthoteran fauna of the Mescalero sands exceeds 40 species. This is also the type locality of *Plagiostira mescaleroensis* Tinkham.

Enemies: a large Jerusalem cricket crawling across open stretches of sandy blowouts must be an attractive morsel for avian predators. The following predators I have seen at the Mescalero Sands: Roadrunner, American Kestrel, Red-tail and Krieder Hawks, Loggerhead Shrike, Burrowing Owl, and Great Horned Owl, all of which are potential enemies of this creature. Nocturnal mammalian predators include coyotes and foxes as well as certain small predatory rodents. On the night of 13 September 1959, shortly after dark I found lying on the sands, 5 miles south of Penwell (near Crane), Texas, a freshly severed, large megacephalic head of a large reddish brown *Stenopelmatus* sp. The probable predator was the Great Plains Grasshopper Mouse (*Onychomys leucogaster articeps*), and the kill was near the western limit of the range of this rodent. Because Highway 380 cuts right through the type locality, some crickets probably are run over at night crossing its two lanes.

Faunal Designation: The newly described *Stenopelmatus* is a member of the Pecos Desert Fauna, which desert is the most northern of three eremological components of the Great Chihuahuan Desert, the other two being the Coahuila Desert immediately to the south and the high elevation Salado Desert of southwestern Neuvo Leon and of northeastern Zacatecas.

## Abbreviated Key to American *Stenopelmatus*

| | | |
|---|---|---|
| 1. | Species completely black, size large | *mescaleroensis* n. sp. |
| | Species small to very large, never completely black | 1 |
| 2(1). | Species large to very large, head and pronotum orange or orange red | 3 |
| | Species medium to small; head and pronotum with variable amounts of black or infuscated | 5 |
| 3(2). | Body completely orange; caudal tibial spine ratio 3 external, 3 internal | *cahuilaensis* Tinkham |
| | Body reddish orange on head and pronotum, abdominal tergites largely black | 4 |
| 4(3). | Internal calcar of caudal tibiae very long and acuminate; caudal tibial spine ratio: 2 external small, 4 internal with two subapical much the largest | *longispina* Brunner |
| | Internal calcar of caudal tibiae longest of the six, their posterior apical portions truncate and spathulate | *fuscus* Haldeman |
| 5(2). | Head and pronotum dorsally shining solid black | *nigrocapitatus* Tinkham & Rentz |
| | Head and pronotum not so | 6 |
| 6(5). | Head and pronotum dorsally with black which is broken up by vertical sutural lines on head and irregularly on pronotum; caudal tibial spine ratio: 2 ext. 3–4 internal | *pictus* Scudder |
| | Entire body infuscated brown, with black abdominal tergites; caudal tibial spine ratio: 2 external, four internal | *intermedius* Davis & Smith |

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# POTENTIAL USE OF GREAT SALT LAKE WATER FOR LOBSTER CULTURE

Roger W. Mickelsen[1], Richard A. Heckmann[1], and Rex C. Infanger[1]

Abstract.— Three experiments were conducted to determine if water from the Great Salt Lake altered in chemical composition and dilution can be used successfully to sustain a species of hermit crab *Pagarus sp.* and the American Lobster (*Homarus americanus*). Great Salt Lake water altered by freshwater dilution will not sustain the hermit crab or the American lobster. Great Salt Lake water can be altered chemically by dilution to support growth of the American lobster.

American lobsters maintained in Instant Ocean synthetic sea water (control) grow at a more rapid rate than animals sustained in altered Great Salt Lake water. A plastic primer coat used for plastic tank repair appears to be a moult inhibitor for the American lobster. Lobsters afflicted by the primer coat are not able to reverse the damage by continued moults.

The American lobster, *Homarus americanus* Milne-Edwards, occurs along the Atlantic Coast of Canada and the United States, where it lives on the continental shelf at depths of 10 to 210 m. Many attempts have been made to culture lobsters to satisfy the rising demand and to supplement decreasing catches (Graham 1973). The most successful work, using natural sea water, is that done at the Massachusetts State Lobster Hatchery. Lobster larvae have been reared with 80 percent survival through the four larval stages (Fig. 1) and grown to market size in two years instead of the normal six years (Hughes, Sullivan, and Shleser 1972).

The Great Salt Lake, in northern Utah, has a salt content 4 to 6 times greater than the world's oceans. As early as 1879, attempts were made to propagate oysters, eels, and marine fish in the estuaries of Great Salt Lake. Failure of these projects was attributed to frequent high winds, which altered the salinity of the estuaries above lethal levels (Miller 1969).

Chemical analyses indicate qualitative similarities between the ionic composition of the Great Salt Lake and sea water, with only quantitative differences as shown in Table 1 (Sverdrup, Johnson, and Fleming 1942). This suggests that water from the Great Salt Lake diluted and altered chemically could support the American lobster.

The objectives of this study are to determine whether (1) chemical additions and various dilutions of water from the Great Salt Lake can support the American lobster, and (2) if alteration of this high saline water can promote growth and a high percentage of survival. Data from these studies will be used as a base for further experimentation to determine if declining supplies of lobsters could be supplemented with this new technique.

## Review of Literature

### Lobster Culture

Life History.— The life history of the American lobster, which is typical of most decapods, is characterized by fertilized eggs developing into larvae which remain as pelagic organisms for a short time before they become benthic organisms.

Dow (1949) determined that copulation occurs within a 48-hour period after the female moults. The initial phase of mating, which occurs in the summer, requires the release of a pheromone by the female. This attracts the male and alters his normally aggressive behavior. According to Hughes and Mathiessen (1962), courtship may require 30 minutes, whereas copulation generally lasts less than five. After copulation the sperm are

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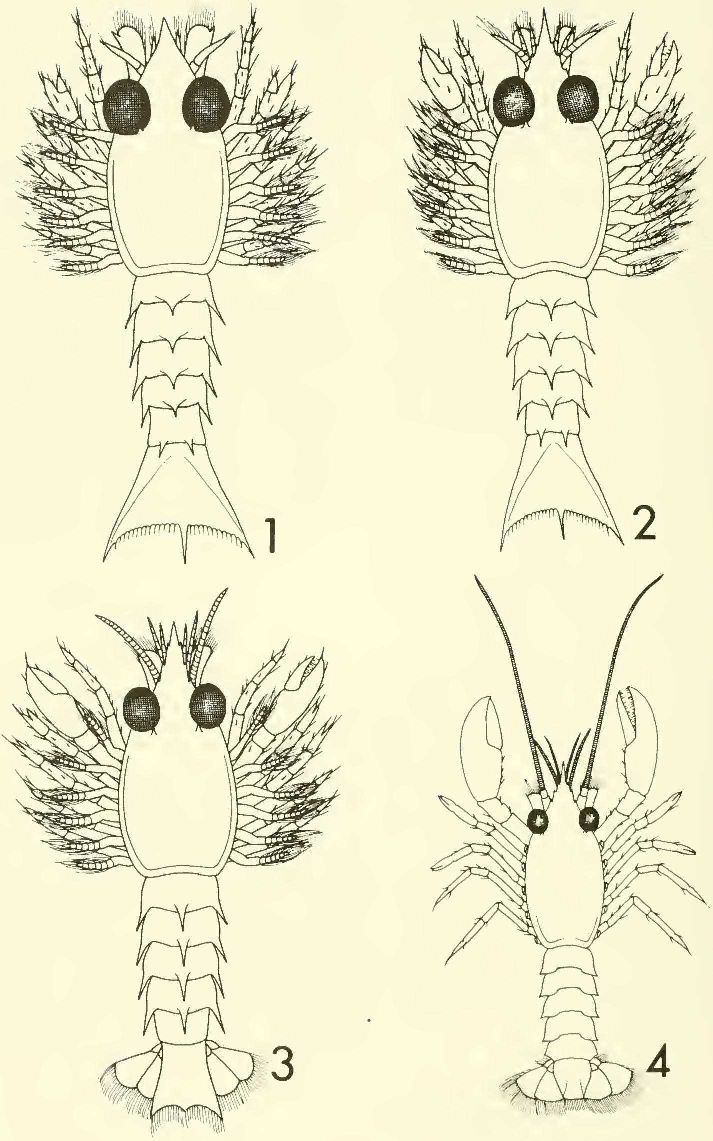

Fig. 1. The first four larval stages of *Homarus americanus* drawn from scanning electron micrographs (Heckmann et al. 1978).

stored in the seminal receptacle while the immature eggs complete development. Bardach, Ryther, and McLarney (1972) estimated that ovulation occurs between 9 and 13 months after copulation; eggs may number 125,000. Sperm fertilize the eggs as they are deposited onto the nonplumose hairs of the swimmerets. The eggs remain glued to the swimmerets for another 10 to 12 months before hatching.

Early in the summer the lobster larvae hatch beneath the female's tail and float away (Hughes 1973). Total time for the larvae to develop and emerge from the eggs is between 19 and 25 months (Bardach, Ryther, and McLarney 1972). Hughes (1973) found that at this point the larvae look like tiny shrimp rather than lobsters, and after three moults they acquire well-developed claws and external morphology of the adult, sink to the bottom, and assume their characteristic benthic existence.

HATCHING AND CARE OF LARVAE.— Lobster culture began in France in 1865 according to Dow (1949), and cultural techniques, which were generally unsuccessful, were developed somewhat later in the 1890s and early 1900s in other countries (Norway, Holland, Great Britain, Canada, Newfoundland, and the United States). Survival of larval lobsters to the fourth stage was still only 4.4 percent in 1947 and 1948 at the U.S. Fish and Wildlife hatchery at Boothbay Harbor, Maine (Dow 1949).

Initial problems encountered by Dow (1949) included the use of (1) brass fittings in water supply systems (copper in brass is highly toxic to lobsters), (2) ambient seawater for hatching systems, and (3) ground liver as a food source. These problems were corrected and survival rates increased when brass fittings were removed from the water supply system, hatchery water was heated, and the liver was replaced with ground mussel.

Larval rearing equipment was improved by Hughes and Matthiessen (1962), who used a plastic circulating tank and a perforated central cylinder placed around a standpipe (Fig. 2), thus removing the need for metallic fittings. Hughes (1973) later modified the apparatus by adding a fiberglass tank with a concave bottom, along with the plastic circulating device (Fig. 2). Larval survival in-

TABLE 1. Comparison of ions present (ppm) in Great Salt Lake water and sea water.

| Ion | Sea water* | Great Salt Lake water** | Ratio |
|---|---|---|---|
| Chlorine | 18,980 | 68,500 | 1:3.6 |
| Sodium | 10,561 | 44,000 | 1:4.2 |
| Sulfate | 2,560 | 8,400 | 1:3.3 |
| Magnesium | 1,272 | 1,703 | 1:1.3 |
| Calcium | 400 | 840 | 1:2.1 |
| Potassium | 380 | 4,000 | 1:10.5 |
| Bicarbonate | 142 | 493 | 1:3.47 |
| Bromine | 65 | trace | |
| Strontium | 13 | trace | |
| Silicate | 0.04–8.6 | 0.0 | |
| Boron | 4.6 | 15.35 | 1:3.3 |
| Flouride | 1.4 | 0.64 | 1:0.45 |
| Aluminum | 0.16–1.9 | unknown | |
| Iron | 0.002–0.02 | 3.8 | 1:1900–1:190 |
| Lithium | 0.1 | unknown | |
| Phosphorus | 0.001–0.10 | 3.45 | 1:3450–1:34.5 |
| Copper | 0.001–0.09 | 0.19 | 1:190–1:2.1 |
| Iodide | 0.05 | unknown | |
| Zinc | 0.005–0.014 | 0.29 | 1:58–1:20.7 |
| Manganese | 0.001 | 0.28 | 1:280 |
| Vanadium | 0.0003 | unknown | |
| Cobalt | 0.0001 | unknown | |

*Sverdrup, Johnson, and Fleming (1942).
**Utah State Department of Health (1972).

creased from 4.4 to 42.6 percent by using this equipment.

GROWTH RATES AND MATING.— Hughes (1972) has shown that sexually mature lobsters can be produced in two to three years by raising water temperatures to 22 C, whereas at ambient temperatures they require between seven and eight years to mature. He also found that, though laboratory mating was relatively easy to accomplish, egg extrusion required a minimum coverage of 46 cm of water (Hughes 1973).

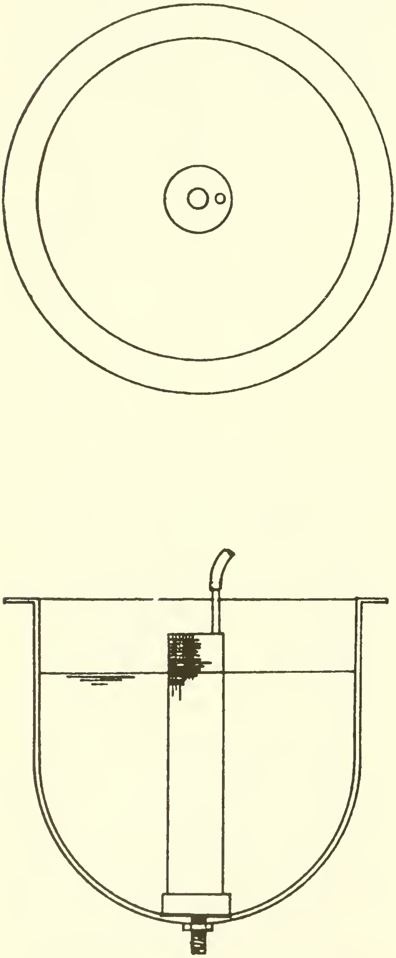

Fig. 2. General views of larval rearing tank (Hughes, Shleser, and Tchobanoglous 1974).

Perkins (1972) demonstrated that, by monitoring the development of the lobster and manipulating the water temperature, embryonic growth could be altered to produce larvae throughout the year. The minimum period of time was 11 months after mating (Bardach, Ryther, and McLarney 1972).

Shleser (1974) has shown that live brine shrimp, *Artemia salina*, produce the highest growth rates of any diet tested for lobster growth to date. Growth rates were improved by Conklin, Devers, and Shleser (1975), who fed the algae *Dunaliella promolecta* to brine shrimp prior to harvesting. Synthetic diets composed of wheat gluten, casein, corn starch, lipids, vitamins, and minerals developed by Conklin, Devers, and Shleser (1975) have produced promising results. However, no diet has yet been formulated to equal the growth rates produced by live brine shrimp.

Gallagher and Brown (1975) observed that synthetic sea water mix, Instant Ocean, produced higher growth rates in juvenile lobsters than did natural sea water. This increased growth may be due to higher pH values maintained in Instant Ocean because of lower bacterial levels.

## Great Salt Lake, Utah

PHYSICAL CHARACTERISTICS.— According to Miller (1969), the Great Salt Lake has a salinity of approximately 105 ppt in the southern half to approximately 250 ppt in the northern half. The Bear, Weber, and Jordan rivers, which account for a majority of the freshwater input, enter the southern half of the lake. According to Stephens (1974), this imbalance of freshwater inflow has caused salt migration to the north arm, resulting in subaqueous precipitation of sodium chloride and a reduction of the salinity of the south.

BIOLOGY.— The Great Salt Lake supports large populations of invertebrates, but no fish. According to several authors (Stephens 1974), brine shrimp (*Artemia salina*), brine flies (*Ephydra hians* and *Ephydra cineria*), waterboatman (*Trichorixa interiores*) (Winget, pers. comm.), 7 species of protozoans (Jones 1946), and 23 species of diatoms (Felix, pers. comm.) are present.

## METHODS AND MATERIALS

GREAT SALT LAKE WATER.— Samples of Great Salt Lake water were collected from the southern half of the lake at the north dike of Silver Sands Marina (Fig. 3). These were returned to Brigham Young University, where they were sealed in five-gallon buckets and stored in darkness.

EXPERIMENTAL ANIMALS.— Hermit crabs were collected from the intertidal zone of the Pacific Ocean near Redondo Beach, California. These were transported to Provo in 5-gallon buckets filled with sea water oxygen-

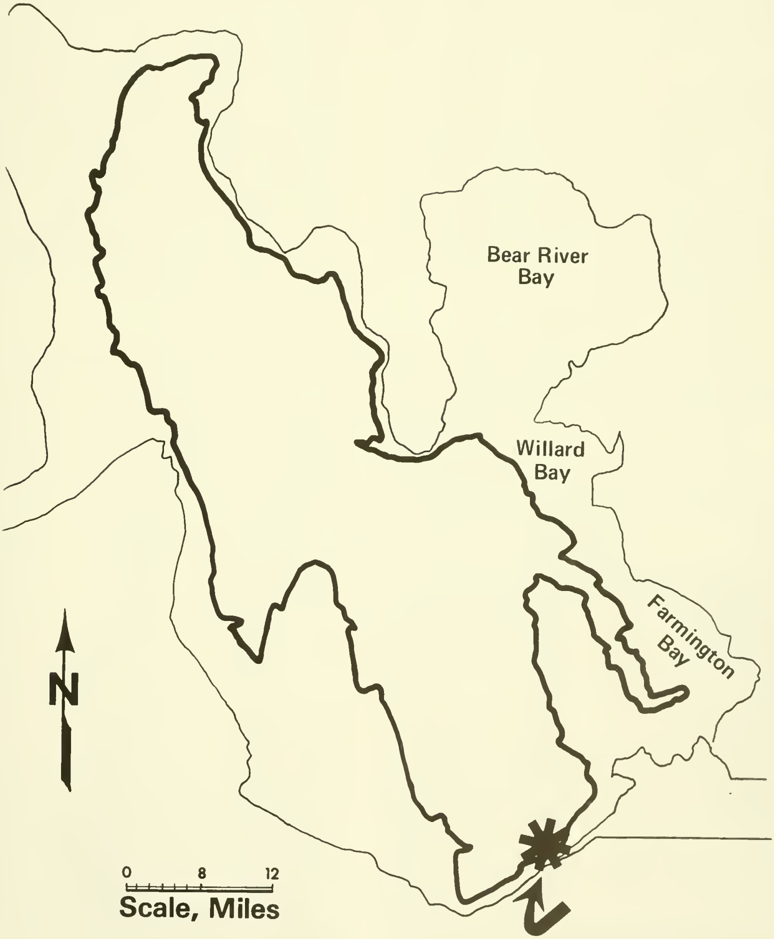

Fig. 3. Sampling site (arrow) for Great Salt Lake water on south shore of Great Salt Lake.

ated with battery-operated aerators. They were maintained at BYU in 20-gallon aquaria filled with Instant Ocean (synthetic sea water) and fed brine shrimp, chopped clams, and frozen shrimp.

Juvenile lobsters were obtained air freight from the Massachusetts State Lobster Hatchery. Animals were packed in large plastic bags filled with sea water and oxygen and placed in styrofoam shipping boxes.

Three different experiments were conducted using juvenile lobsters and hermit crabs. Animals in all experiments were fed and observed daily. Data were collected concerning disease, behavior, food consumption, and survival.

EXPERIMENT I.— Chemical analysis of the Great Salt Lake water (Utah State Department of Health) indicated that the chemical composition was similar to sea water (Table 1). These data also indicated that a freshwater dilution by a factor of 3 would create a situation similar in both composition and concentration (Table 2).

A mixture with a salinity of 34 ppt was prepared by adding one part Great Salt Lake water to two parts tap water. The mixture was placed in a 37-liter aquarium equipped with an undergravel filter with calcium carbonate as the substrate. Five hermit crabs were placed in the aquarium.

EXPERIMENT II.— One part of Great Salt Lake water was diluted with 9.7 parts tap water. This dilution reduced the potassium ion concentration to 380 ppm, the amount found in sea water (Table 2). Chemical compounds that were added to adjust the ionic concentrations of the mixture back to levels equivalent with sea water were: sodium chloride, sodium sulfate, magnesium chloride, calcium chloride, sodium bicarbonate, sodium bromide, sodium phosphate, sodium molydate, lithium chloride, sodium iodide, aluminum chloride, vanadyl chloride, and cobaltous chloride. The mixture was then placed in two 37-liter aquaria with perforated plastic dividers. Two lobsters were

TABLE 2. Comparison of ions present (ppm) in sea water, diluted Great Salt Lake water 1:3 and 1:8.7, and an updated analysis of Great Salt Lake water.

| Ion | Sea water[1] mg/l | Diluted Great Salt Lake water[2] 1:3 mg/l | Diluted Great Salt Lake water 1:8.7 mg/l | Updated analysis Great Salt Lake water[3] mg/l | Updated analysis diluted 1:9.7 mg/l |
|---|---|---|---|---|---|
| Chloride | 18,980 | 17,125 | 6,523.8 | 57,982.0 | 5,977.52 |
| Sodium | 10,561 | 11,000 | 4,190.5 | 28,813.0 | 2,970.41 |
| Sulfate | 2,560 | 2,100 | 800.0 | 12,500.0 | 1,288.65 |
| Magnesium | 1,272 | 425.8 | 162.2 | 3,360.0 | 346.39 |
| Calcium | 400 | 210 | 80.0 | 244.0 | 25.15 |
| Potassium | 380 | 1,000 | 380.1 | 3,700.0 | 381.44 |
| Bicarbonate | 142 | 123.3 | 47.0 | 299.0 | 30.82 |
| Bromine | 65 | trace | trace | 0.09 | 0.01 |
| Strontium | 13 | trace | trace | 0.04 | 0.004 |
| Silicate | 0.04–8.6 | 0.0 | 0.0 | 4.6 | 0.47 |
| Boron | 4.6 | 3.83 | 1.7 | 18.0 | 1.85 |
| Flouride | 1.4 | 0.16 | 0.06 | 8.2 | 0.84 |
| Aluminum | 0.16–1.9 | unknown | unknown | 0.24 | 0.02 |
| Iron | 0.002–0.02 | 0.95 | 0.36 | 0.13 | 0.013 |
| Lithium | 0.1 | unknown | unknown | 16.10 | 1.66 |
| Phosphorus | 0.001–0.1 | 0.87 | 0.32 | 24.5 | 2.53 |
| Copper | 0.001–0.09 | 0.05 | 0.09 | 0.05 | 0.005 |
| Iodide | 0.05 | unknown | unknown | 0.46 | 0.005 |
| Zinc | 0.005–0.014 | 1.16 | 0.03 | 0.14 | 0.014 |
| Manganese | 0.001 | 0.07 | 0.27 | 0.15 | 0.015 |
| Vanadium | 0.0003 | unknown | unknown | 0.03 | 0.003 |
| Cobalt | 0.0001 | unknown | unknown | 0.29 | 0.029 |

[1] Sverdrup, Johnson, and Fleming (1942).
[2] Utah State Department of Health (1972).
[3] Ford Chemical Laboratory and Western Standard Laboratory (1976).

placed in each of the aquaria and fed a diet of frozen brine shrimp.

EXPERIMENT III.— Great Salt Lake water was diluted by adding 9.7 parts distilled water to one part Great Salt Lake water. The ionic concentration was adjusted to levels consistent with sea water by addition of sodium chloride, magnesium chloride, calcium chloride and sodium bicarbonate. No further ions were added inasmuch as a chemical analysis indicated that the concentration of all other ions being considered was greater than or equal to the amounts found in sea water (Table 2). The mixture was then placed in four tanks, each 70 cm long, 40 cm wide, and 15 cm deep, constructed of glass and acrylic plastic. Dividers of acrylic plastic 1.25 mm thick were used to separate each tank into 28 compartments, each 10.2 cm square. Individual tanks were filled to a depth of 7.6 cm with broken oyster shells to serve as a biological filter and buffer for the water circulating through the tank.

Groups of four tanks were connected to a single centrifugal pump by pipes 1.25 cm in diameter. The outflow from the pump was divided into eight 1.25 cm PVC pipes. Two pipes, each with two 0.31 cm holes drilled 10 cm apart, were supported over each tank to provide an individual water supply for each compartment (Fig. 4).

Instant Ocean was mixed and added to the remaining four tanks. Water changes were made in both systems at a rate of 25 percent per month to maintain high pH values.

To enhance the growth of nitrifying bacteria, 7 ppm ammonium chloride was added to the water. When chemical tests revealed that ammonia had been completely oxidized to nitrate, the system was considered safe for the addition of experimental animals.

Juvenile lobsters were acclimatized and, upon arrival, one was placed in each 10.2 square compartment. All animals were fed frozen brine shrimp to satiety on a daily basis. Uneaten food was removed from the compartments before the next day's feeding.

A dissecting microscope with an ocular micrometer was used to measure the carapace length of each lobster after a two-week acclimation period and after 60 days.

Salinity, temperature, pH, nitrite, and dissolved oxygen levels were measured daily with appropriate meters. Nitrite was measured with a Bausch and Lomb Spectrophotometer.

## RESULTS

EXPERIMENT I.— The five hermit crabs subjected to diluted Great Salt Lake water all died within days after introduction. No feeding was observed by any of the animals during the experimental period. An unusual arrhythmic contraction of the appendages of the crabs was noted after three days of exposure to the mixture.

EXPERIMENT II.— The four American lobsters reared in altered Great Salt Lake water all survived for 45 days. The lobsters died pe-

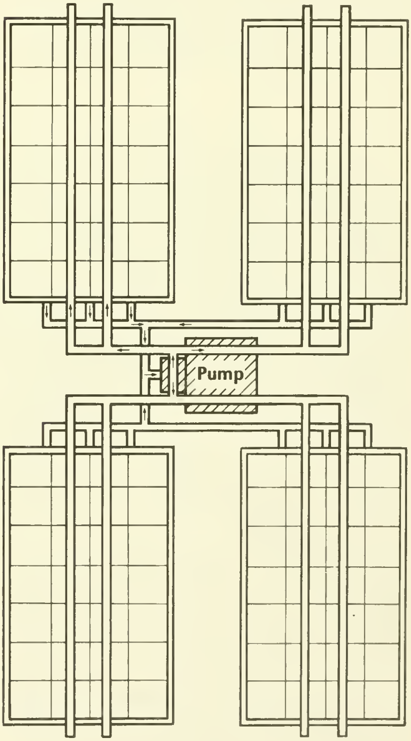

Fig. 4. Experimental aquaria system showing four tanks interconnected by a single pump.

riodically after the initial 45 days, with one animal surviving for 97 days in the altered Great Salt Lake water.

All animals manifested similar symptoms before death, which included self-induced amputation of one or both of the large front claws, and a light blue exoskeleton which became soft and flexible.

Experiment III.— Lobsters maintained in artificial sea water prepared from Instant Ocean displayed 16 percent more growth than those lobsters reared in altered Great Salt Lake water (Table 3).

Results of water quality analysis are presented in Table 4. These data indicate that water quality during the experiments was acceptable for lobster maintenance.

Mortality occurred in both water types when the animals attempted to moult (Fig. 5). This occurred after Dow Corning primer coat 1206 was used to repair leaking aquaria.

## Discussion

Experiment I.— Great Salt Lake water in which the salinity had been reduced to 34 ppt was lethal to the hermit crab *Pagurus sp.* Toxicity may have been due to a high potassium ion concentration and low calcium and magnesium ion concentrations produced by salinity reduction (Guyton 1971) (Table 2). The potassium ion was approximately three times the level normally found in sea water, whereas calcium and magnesium ion concentrations were ½ and ⅓ of corresponding values. High potassium ion concentrations may have placed stress on the invertebrate nervous system by increasing the extracellular potassium ion concentration, thus thwarting nerve depolarization.

Muscle activity may have been affected by low extracellular calcium and magnesium. According to Guyton (1971) low levels of calcium may have decreased the ability of the heavy meromyosion (HMM) to "bridge" with G-actin molecules. Insufficient magnesium ion may have further compounded the problem by inhibiting calcium ion transmission into muscle tissue, and increasing muscle contraction and irritability (Guthrie 1975).

Nervous and muscular interference due to ionic imbalances may have been demonstrated by the frequent sporadic flexure of the appendages by the crabs.

Experiment II.— Alteration of Great Salt Lake water by freshwater dilution and dry chemical addition produced a medium which supported the American Lobster for short periods of time. However, the death of the animals between 45 and 90 days suggests that the medium and the physical conditions were far from adequate. Loss of the large anterior claws, slow moulting, and soft flexible exoskeletons also suggest that diet, and/or physical environment, contributed to the degenerative condition of the experimental lobsters.

Experiment III.— The average increase in carapace length for lobsters grown in altered Great Salt Lake water was 29.75 percent, but was 46.0 percent for those grown in Instant Ocean. Statistical analysis of each group showed no significant difference between individual tanks of each type of water, but a highly significant difference between water types at the 0.05 confidence level. Average water quality parameters for both types of

Table 3. Average carapace lengths for 28 lobsters per tank cultured in Instant Ocean and altered Great Salt Lake water for a 60-day period.

| Tank | Beginning lengths mm | Finishing lengths mm | % increase |
|---|---|---|---|
| Instant Ocean | | | |
| 1 | 6.56 | 9.49 | 44 |
| 2 | 6.61 | 9.53 | 44 |
| 3 | 6.34 | 9.55 | 50 |
| 4 | 6.45 | 9.47 | 46 |
| Altered Great Salt Lake water | | | |
| 1 | 6.07 | 7.89 | 29 |
| 2 | 5.78 | 7.81 | 35 |
| 3 | 5.37 | 7.11 | 32 |
| 4 | 6.24 | 7.68 | 23 |

Table 4. Average water quality data for Instant Ocean and altered Great Salt Lake water for the 60-day experimental period.

| Measurement | Instant Ocean | Great Salt Lake |
|---|---|---|
| Dissolved oxygen | 6.95 ppm | 7.09 ppm |
| Salinity | 33.06 ppt | 33.85 ppt |
| pH | 7.9 | 7.9 |
| Temperature | 21.9 C | 21.7 C |
| Nitrite | 0.0 ppm | 0.0 ppm |

water were within the acceptable ranges proposed by Spotte (1970) and Hughes, Sullivan, ans Shleser (1972).

Survival data for animals held in each water type was not useful because of sudden mortality in both water systems which occurred after the repair of leaks with Dow Corning 1206 primer coat. Although the plastic primer had serious affects on some lobsters, others appeared to be unaffected and continued to feed and grow normally. Most of the lobsters were found dead in a partially moulted condition. The cause for death during this process may have been due to asphyxiation caused by the old shell pinching the new softer shell over the gills, thus inhibiting water flow. Those animals which moulted successfully did not die immediately, but wasted away for several months. In some cases the old shell was shed successfully except for the walking legs, claws, or tail. These animals frequently became cripples because the new shell hardened in odd shapes and positions. Animals which had undergone incomplete ecdysis displayed normal responses to food and seemed to eat normally. In some cases these animals lived for comparatively long periods of time and moulted as many as three times. In no case, however, did the animals ever regenerate a normal shell.

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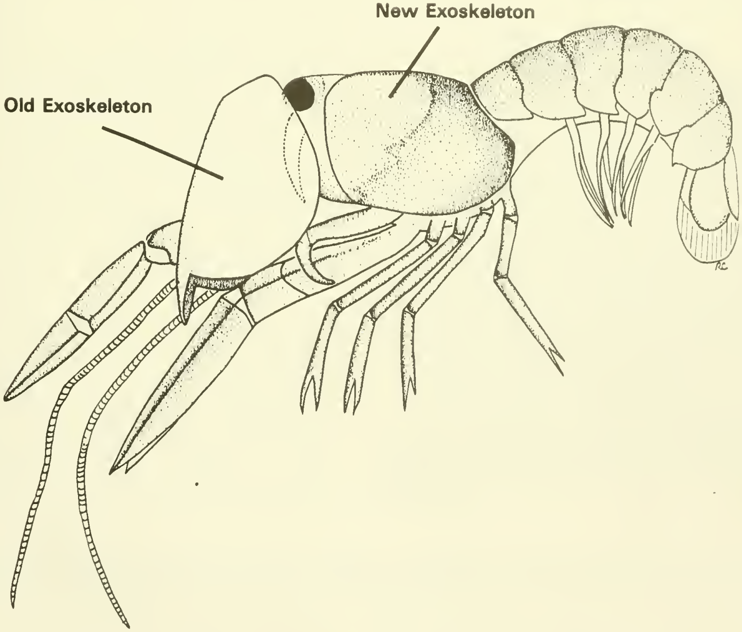

Fig. 5. Artist's drawing of lobsters experiencing incomplete moulting syndrome.

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# NEARCTIC STONEFLY GENERA AS INDICATORS OF ECOLOGICAL PARAMETERS (PLECOPTERA: INSECTA)[1]

Richard W. Baumann[2]

ABSTRACT.— Selected stonefly genera found in North America are classified as to their occurrence in: cold lotic, warm lotic, or lentic habitats. Most genera occur only in the cold lotic, but several occur both in cold and warm lotic systems. Few are found exclusively in warm lotic habitats and almost none in lentic. Lake or true lentic inhabits are found to usually be cold lotic species which have adapted to life in the wave-washed shores of cold mountain lakes.

Even though data at the specific level would be even more useful, especially where different faunal regions are involved, stoneflies are probably the best insect indicators of aquatic environmental quality at the generic level.

Illies (1970) presented the idea that the genus is the basic taxonomic unit of ecology and that systematists could gain valuable data for use in their classification of taxa by obtaining an understanding of the ecological requirements of the organism being studied. The converse should then also be true. If the phylogeny determined through the analysis of the systematics of a group is correct, then ecologists can predict the type of habitat present from a knowledge of the genera that live there.

Because environmental factors exert the selection pressure on populations that may cause some of them to evolve into new species, a level of habitat characterization must be reached that is narrow enough to be useful but broad enough to encompass large genera. Wiggins and Mackay (1978) classified the extant Nearctic Plecoptera, Ephemeroptera, and Trichoptera genera according to their occurrence in cold and warm lotic and/or lentic habitats. Their results for the Plecoptera showed that most genera occur in cold lotic waters, with decreasing numbers found in warm lotic and lentic habitats, respectively. However, they did not delineate those genera which occur in more than one habitat. Because such information is important, example genera were selected from each family and more complete data recorded.

Stoneflies were noted by Gaufin (1973) to be good indicators of water quality. However, their presence or absence alone is not enough on which to base any final conclusions. Some species are able to escape harsh conditions by emerging during the winter, when temperatures are low; others survive in microhabitats such as the rocky shores of lakes and small spring seeps. This makes it necessary to understand the biology of the species involved before conclusions can be drawn.

## MATERIALS AND METHODS

The nearctic stonefly fauna (Baumann 1976) was divided first into the groups Euholognatha and Systellognatha. These groups were then studied one family at a time, with an emphasis being placed on the common or most abundant genera.

Four ecological groupings were defined and characterized as shown in Figure 1. The two flowing water or lotic systems were divided according to mean temperature. No conclusive experimental data were available, so the 16 C isotherm is not final, but was chosen as a useful point of separation.

The lentic systems were likewise divided, but very little is known about the biology of stoneflies which occur in lentic habitats. The availability of proper substrate is, however, important.

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[1] Presented at the workshop on indicator communities held at the North American Benthological Society meetings in Winnipeg, Manitoba, May 1978.

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Stream order classifications based on the Stream Continuum Theory of Cummins (1973) were included in an attempt to relate the functional ecology of the organisms occurring in lotic habitats.

Because published data about the occurrence of stoneflies is not available for many species, the field experience of the author in many parts of North America was relied upon heavily.

## Results

No stonefly genera occur in warm lentic habitats, probably because of the low oxygen level. Although most genera occur primarily in cold lotic habitats, there is a strong correlation even at the family level with adaption for existence in warm lotic or cold lentic habitats. For this reason, results are here presented according to systematic group and one family at a time.

The group Euholognatha consists of essentially herbivorous families which feed on detritus and plant material. The data (Fig. 2) show that most genera contain species which are found in cold lotic or cold lentic habitats. These habitats correspond ecologically to the functional classifications of Cummins from 1–6.

Cold lotic habitats are most often colonized by members of the family Nemouridae. These habitats occur at high altitudes or in spring-fed areas where temperatures remain cool throughout the year. Some species even survive in lakes, ponds, or swamplike areas with predominantly silt bottoms if some dead trees occur and provide a suitable substrate.

Genera in the Capniidae often have species which occur in warm lotic habitats. These species are only found in the nymph or adult stage during the cold winter months. They go into a diapause in the warm months, as noted by Khoo (1968). Several capniid species also occur in very northern arctic localities, where they emerge during late summer, when conditions are most favorable. Some species, including several members of the genus *Capnia*, are found in lakes at high altitudes and seem to emerge and complete their life cycle when the ice breaks. Only one species, *Capnia lacustra* Jewett (Nebeker and Gaufin), is strictly confined to a lotic habitat (Frantz and Cordone 1966).

| Ecological Groupings | Habitat Characterization |
|---|---|
| Cold Lotic | Streams, creeks and rivers with mean temp. below 16 C; Includes orders 1-6. |
| Warm Lotic | Primarily rivers with mean temp. which often exceeds 16 C during warm months; Includes orders 7-12. |
| Cold Lentic | Ponds and lakes usually at high altitudes which never exceed 16 C in temp. Wave action and correct substrate also necessary. |
| Warm Lentic | Ponds and lakes which often exceed 16 C in temp. Bottom composed of sand, silt or other loose material. |

Fig. 1. Ecological groupings and characterization of corresponding habitats based on stoneflies (Plecoptera: Insecta).

Many species in the family *Taeniopterygidae* occur in large rivers. The two most common North American genera, *Taeniopteryx* and *Taenionema*, contain several seemingly environmentally hardy species. Some occur in the large, silt-laden rivers of the West and others occur in the slow, sluggish bayous of the Southeast.

The Leuctridae are primarily found in clear, cold streams, but a few species do occur in large rivers.

The group Systellognatha (Fig. 3) contains two mainly herbivorous families, Peltoperlidae and Pteronarcyidae; two carnivorous families, Perlodidae and Perlidae; and the omniverous family, Chloroperlidae.

Members of the family Peltoperlidae are not well distributed in the nearctic region. They are found mostly in the Coast and Cascade mountains of the West and the Appalachian Mountains of the East, in small streams or creeks of good water quality.

The Pternoarcyidae are large in size and generally occur in large rivers. However, such species as *Pteronarcys princeps* (Banks) have adapted to life in the small streams of the Pacific Northwest, and the eastern genus *Allonarcys* is found commonly in small creeks.

The family Perlodidae contains many gen-

| Family and Genus | Cold Lotic | Warm Lotic | Cold Lentic | Warm Lentic |
|---|---|---|---|---|
| Nemouridae | | | | |
| *Amphinemura* | + | + | + | 0 |
| *Malenka* | + | 0 | + | 0 |
| *Nemoura* | + | 0 | + | 0 |
| *Ostrocerca* | + | 0 | 0 | 0 |
| *Podmosta* | + | 0 | + | 0 |
| *Shipsa* | + | 0 | 0 | 0 |
| *Zapada* | + | 0 | + | 0 |
| Capniidae | | | | |
| *Capnia* | + | + | + | 0 |
| *Isocapnia* | + | 0 | 0 | 0 |
| *Mesocapnia* | + | + | 0 | 0 |
| *Utacapnia* | + | + | 0 | 0 |
| Taeniopterygidae | | | | |
| *Taenionema* | + | + | 0 | 0 |
| *Taeniopteryx* | + | + | 0 | 0 |
| Leuctridae | | | | |
| *Leuctra* | + | + | 0 | 0 |
| *Megaleuctra* | + | 0 | 0 | 0 |
| *Paraleuctra* | + | 0 | 0 | 0 |

Fig. 2. Ecological groupings for the most common genera in the stonefly families of the Euholognatha. + = occurs, O = does not occur.

| Family and Genus | Cold Lotic | Warm Lotic | Cold Lentic | Warm Lentic |
|---|---|---|---|---|
| Peltoperlidae | | | | |
| *Peltoperla* | + | 0 | 0 | 0 |
| *Yoraperla* | + | 0 | 0 | 0 |
| Pteronarcyidae | | | | |
| *Allonarcys* | + | + | 0 | 0 |
| *Pteronarcys* | + | + | 0 | 0 |
| Perlodidae | | | | |
| *Arcynopteryx* | + | 0 | + | 0 |
| *Cultus* | + | + | 0 | 0 |
| *Diura* | + | 0 | + | 0 |
| *Isogenoides* | + | + | 0 | 0 |
| *Isoperla* | + | + | 0 | 0 |
| *Hydroperla* | + | + | 0 | 0 |
| *Megarcys* | + | 0 | 0 | 0 |
| Perlidae | | | | |
| *Acroneuria* | + | + | 0 | 0 |
| *Calineuria* | + | + | 0 | 0 |
| *Claassenia* | + | + | 0 | 0 |
| *Hesperoperla* | + | + | + | 0 |
| *Neoperla* | + | + | 0 | 0 |
| *Paragnetina* | + | + | 0 | 0 |
| *Perlesta* | + | + | 0 | 0 |
| Chloroperlidae | | | | |
| *Alloperla* | + | 0 | 0 | 0 |
| *Paraperla* | + | 0 | + | 0 |
| *Suwallia* | + | 0 | 0 | 0 |
| *Sweltsa* | + | 0 | 0 | 0 |

Fig. 3. Ecological groupings for the most common genera in the stonefly families of the Systellognatha. + = occurs, O = does not occur.

era which contain few species. They are carnivores and are generally not common in most systems. Several genera such as *Hydroperla* have, however, become very successful in areas where few stoneflies occur because they are able to take advantage of the food resources available but escape the harsh conditions by a diapause of some kind (Oberndorfer and Stewart 1977). Some genera such as *Arcynopteryx* and *Diura* are very successful in cold lakes at northern latitudes.

Most genera in the Perlidae have species that occur in large, warm rivers. Such genera as *Perlesta* and *Neoperla* occur in areas where no other stoneflies can exist and emerge and complete their life cycles during the hottest part of the year. Only the western genus *Hesperoperla* is known to have adapted to life in spring-fed ponds.

Chloroperlidae are generally very sensitive to environmental eutrophication and occur only under very favorable conditions. They are generally only found in cold lotic systems. *Paraperla frontalis* (Banks) has, however, been collected at or near the mouth of several lakes in Glacier National Park and also in the Canadian Rockies.

## DISCUSSION

Stoneflies are useful as indicators of environmental quality at the generic level. Such families as Leuctriidae and Chloroperlidae contain mostly genera which can survive only in cold lotic habitats. However, other families such as Perlodidae and Perlidae have many species that are well adapted to life in warm lentic environments.

Care must be taken to understand the environmental requirements of each species. Often *Neoperla* species occur in headwater streams as well as large rivers, and *Hesperoperla pacifica* (Banks) occurs in springfed streams, creeks, and large rivers. Such genera as *Capnia* and *Arcynoteryx* do not seem to support the idea that the genus is an ecological entity because they contain species that occur both in lotic and lentic habitats. However, when the requirements of the species that occur in the cold lotic systems are examined, they are found to be the same but are simply supplied by waves washing the shore instead of a flowing current.

At the present time, no stoneflies are known to occur in warm lotic habitats in North America.

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# COMPETITIVE DISPLACEMENT AS A FACTOR INFLUENCING PHYTOPLANKTON DISTRIBUTION IN UTAH LAKE, UTAH

Lorin E. Squires[1], Mark C. Whiting[2], Jack D. Brotherson[1], and Samuel R. Rushforth[1]

Abstract.— Phytoplankton studies during the summer of 1974 in Utah Lake, Utah, demonstrated the development of disjunct distributions of *Aphanizomenon flos-aquae* and *Ceratium hirundinella.* Differential response to environmental factors and competitive displacement are proposed as probable explanations for this phenomenon.

Theoretically, competitive displacement among organisms has occurred and is still occurring in all ecosystems. In terrestrial systems and particularly in plant communities, this process is often difficult to observe directly because these communities change so slowly through time. In most such communities, competition between organisms has undoubtedly contributed at some time to differential resource utilization and thus to separate niche development. Because environmental partitioning leads to a decrease in competition, the occurrence of competitive displacement has subsequently declined. However, in ecosystems where generation times are short, and successional sequences occur seasonally, community interactions are rapid and new settings are frequently provided for competitive confrontation. Phytoplankton systems exemplify such conditions and thus provide a possible arena for competitive displacement to be observed.

Competitive displacement has been of interest since the time of Darwin (1859), but has received greater attention and investigation in the last 30 to 40 years (Hardin 1960) following Gause's experimental evidence that no two species can exist indefinitely in the same niche (Gause 1969). Gause claimed that "as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has advantage over its competitor." Additional refinement of this idea was presented by Hardin (1960), who suggested that if two sympatric noninterbreeding populations occupy the same ecological niche, the population with the breeding advantage will eventually displace the other.

The conditions necessary for competitive displacement to occur can be summarized as follows. First, environmental equilibrium must occur. Second, environmental equilibrium must last long enough for exclusion or displacement to occur. Third, in order to compete, species must use some of the same resources. And fourth, species using the same resources must have high enough densities for competition to occur.

Several recent ecological studies have attempted to define specific niche boundaries for sympatric species and demonstrate partitioning of the environment in terms of time, space, or food materials (MacArthur 1958, Jaeger 1971, Schoener 1968, Miracle 1974, Makarewicz and Likens 1975). Such partitioning leads to reduced interspecific competition, thus allowing species to coexist without displacement of one or the other. However, phytoplankton studies have been cited as demonstrating a possible exception to partitioning and niche separation. Hutchison (1961) termed this phenomenon the "paradox of the plankton" because a high diversity of phytoplankton organisms coexist in an apparently homogenous limnetic environment.

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A number of theories have been introduced to explain planktonic systems. Hutchinson (1961) submitted that environmental equilibrium is not achieved because of highly fluctuating lentic environments and the short generation time of most plankton organisms. Richerson et al. (1970) postulated a plankton habitat of contemporaneous heterogeneity that is transitory in time. They suggested that certain species would have competitive advantage in each of the various contemporaneous patches in a lake's epilimnion. Petersen (1975) explained planktonic diversity by relating it to differential nutrient uptake. Titman (1976) demonstrated with laboratory experiments that Petersen's theory was plausible for at least the two plankton species *Cyclotella meneghiniana* and *Asterionella formosa*. Levandowsky (1972) presented the various causal factors affecting the plankton in terms of linking, separating, rarifying, reinforcing, and variational factors and suggested that biologists should widen their view in searching for explanations for plankton dynamics and diversity.

This paper reports the occurrence of two phytoplankters, *Ceratium hirundinella* and *Aphanizomenon flos-aquae*, which coexisted temporally in Utah Lake during the late summer of 1974 but became spatially disjunct. Competitive displacement is proposed as one factor causing the segregation of these species.

## UTAH LAKE PHYTOPLANKTON

During the summer months of 1974, studies of the phytoplankton communities of Utah Lake, Utah (Whiting et al. 1978), were performed. We particularly examined seasonal succession and concomitant changes in environmental parameters. We found that the early summer communities were composed of a diverse group of diatoms and green and blue-green algae. During the same period of time, the environment in the lake was more heterogenous than at any other time. As the season progressed, environmental variation and algal diversity both decreased (Fig. 1). By August, algal communities were very homogenous, being composed of *Aphanizomenon flos-aquae* and *Ceratium hirundinella* almost exclusively. At that time, these two species comprised from 89 to 100 percent of the algal standing crop at our sampling sites.

While making field collections on 15 August 1974, we noticed that the distribution of *Aphanizomenon flos-aquae* and *Ceratium hirundinella* had become disjunct. Calculation of relative densities of the two species and plotting their occurrence against each other confirmed spatial separation between the two (Fig. 2). Many stands were essentially unialgal. To assess any relationship between environmental parameters and distribution of these two species, we subjected the data to discriminant analysis (Klecka 1975). The discriminate function separated the two species completely on the basis of seven environmental variables (pH, phosphate [$PO_4$], Mg hardness, water temperature, total hardness, dissolved oxygen, and alkalinity). By far the most significant of these was pH. When the pH variable was removed and the stands were reevaluated, 100 percent environmental separation still existed between the two communities. However, upon examining the important discriminators, we became convinced that they were effects of the disjunct species distribution rather than causes. For instance, photosynthesis in aquatic systems often has the effect of increasing pH (Cole 1975). Consequently, the increased standing crop (Fig. 3) and thus elevated net photosynthesis in the *A. flos-aquae* stands would account for the higher pH and temperature levels in these stands. Furthermore, elevated pH and temperature levels are known to enhance precipitation of magnesium carbonates (Stum and Morgan 1970, Harvey 1969), which could account for lower measurable levels of magnesium hardness and total hardness in the same stands.

Correlation analyses (Snedecor and Cochran 1967) failed to indicate differential preferences of the two species for any of the variables identified in the discriminant analysis. The results of these analyses showed that abundance of both *A. flos-aquae* and *C. hirundinella* was positively correlated with the same environmental variables (turbidity, salinity, phosphate, pH and water temperature: $\alpha = .01$). This evidence, coupled with the increased lake homogeneity observed in mid-August (Fig. 1), suggests that the two algal species may have been occupying the same environmental niche at that time. Thus, conditions were such that competitive exclusion or displacement could operate in the system.

It occurred to us that it might be possible to analyze competitive displacement using the niche overlap methods of Colwell and Futuyma (1971). Thus, we plotted niche breadth through the summer for each species (Fig. 4). The results indicated that *Ceratium* had a greater niche breadth than *Aphanizomenon* in early summer, but that the reverse was true later in the summer. Spatial niche overlap analysis for these two algae was also plotted against time (Fig. 5). Niche overlap was low in the early summer when standing crop was low enough that the two species rarely occurred together in appreciable numbers. As the summer progressed, spatial niche overlap increased as standing crop increased in a tight linear relationship ($R^2 = .88$). However, between early and middle August, a major reduction in spatial niche overlap occurred so that the last data point (15 August) showed as little overlap as in the earliest summer communities. Colwell and Futuyma (1971) maintained that a high degree of overlap indicates a joint use of resources, whereas low overlap indicates low levels of resource sharing. They also stated

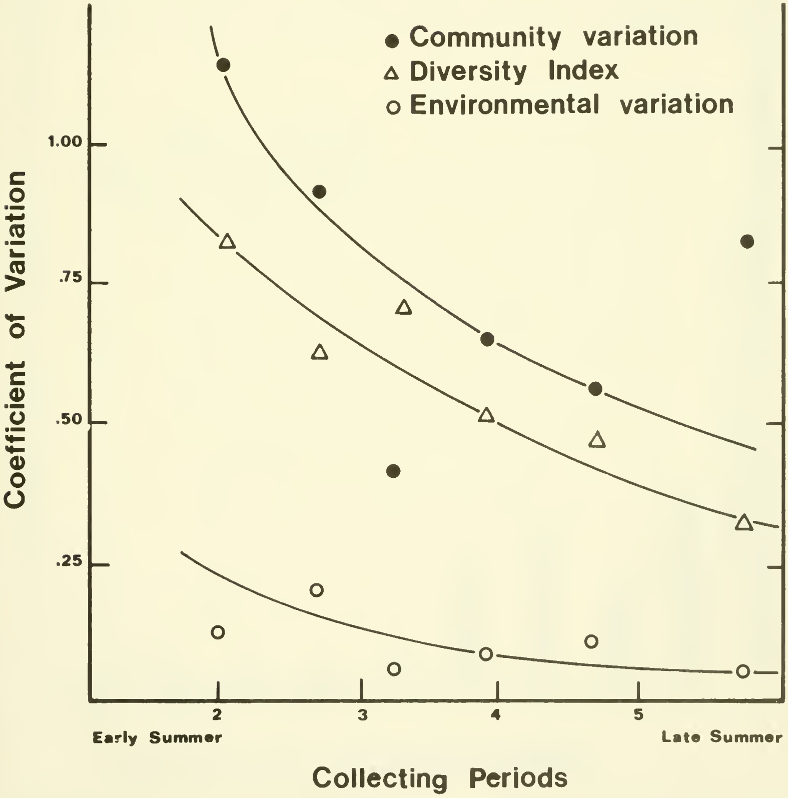

Fig. 1. Environmental and algal community gradients in Utah Lake, Utah, from 6 June to 15 August 1974.

that competitive displacement tends to reduce niche breadth and overlap among competing species. The niche breadth and overlap measurements of *C. hirundinella* and *A. flos-aquae* through summer 1974 in Utah Lake reflected just such conditions. The reduction in niche overlap observed on 15 August occurred concurrently with an exponential increase in the standing crop of *A. flos-aquae* (Fig. 3). These facts, plus the narrowed niche breadths for both *Aphanizomenon* and *Ceratium*, provide strong evidence for competitive displacement.

Two other explanations exist which could account for the disjunct distribution of these organisms that developed in August. The first is seasonal succession and the second is some unmeasured environmental variable creating a heterogenous environment.

Seasonal succession occurs when changes caused by progression of the season create new environmental conditions that promote the development of some species and depress the development of others. While competition is a factor in the interspecific relationship that occurs during seasonal succession, competitive displacement as such is largely due to changes in niche characteristics. Our niche breadth analysis (Fig. 4) shows that *C. hirundinella* reached a maximum breadth in July and thereafter declined, and *A. flos-aquae* reached a maximum breadth somewhat later. Even so, the actual standing crop of *C. hirundinella* increased from July through August, and in none of the samples were dead or dying cells encountered. Therefore, because the population of *Ceratium* showed no signs of decline, we con-

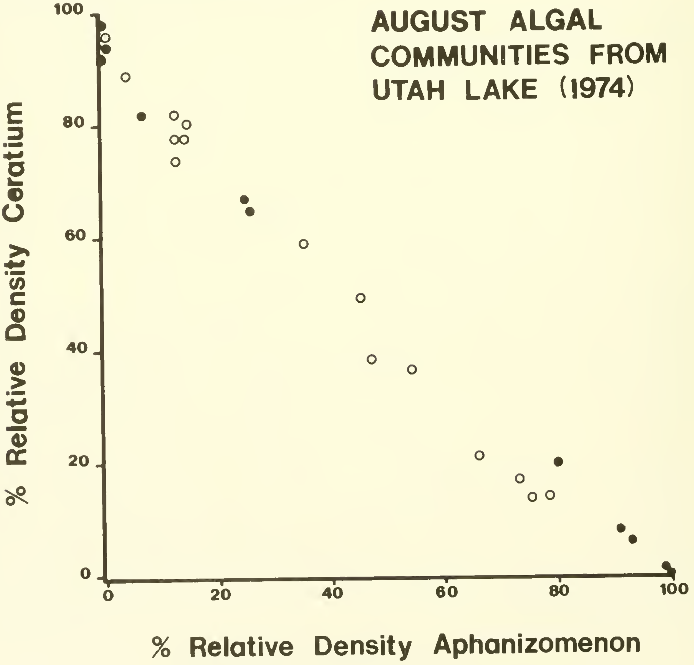

Fig. 2. Percent relative density of *Aphanizomenon flos-aquae* plotted against *Ceratium hirundella* for August 1974 algal communities. Clear circles designate 8 August collections; solid circles designate 15 August collections.

clude that the disjunct distribution was not due to seasonal replacement of *Ceratium* by *Aphanizomenon.*

The homogeneity of the limnetic environment in Utah Lake during late summer has already been discussed. However, the importance of wind and water currents in creating distributional patterns in the lake were not closely analyzed. The authors have noted for several years that during algal blooms in Utah Lake, local heavy concentrations of algae can develop, often taking the form of

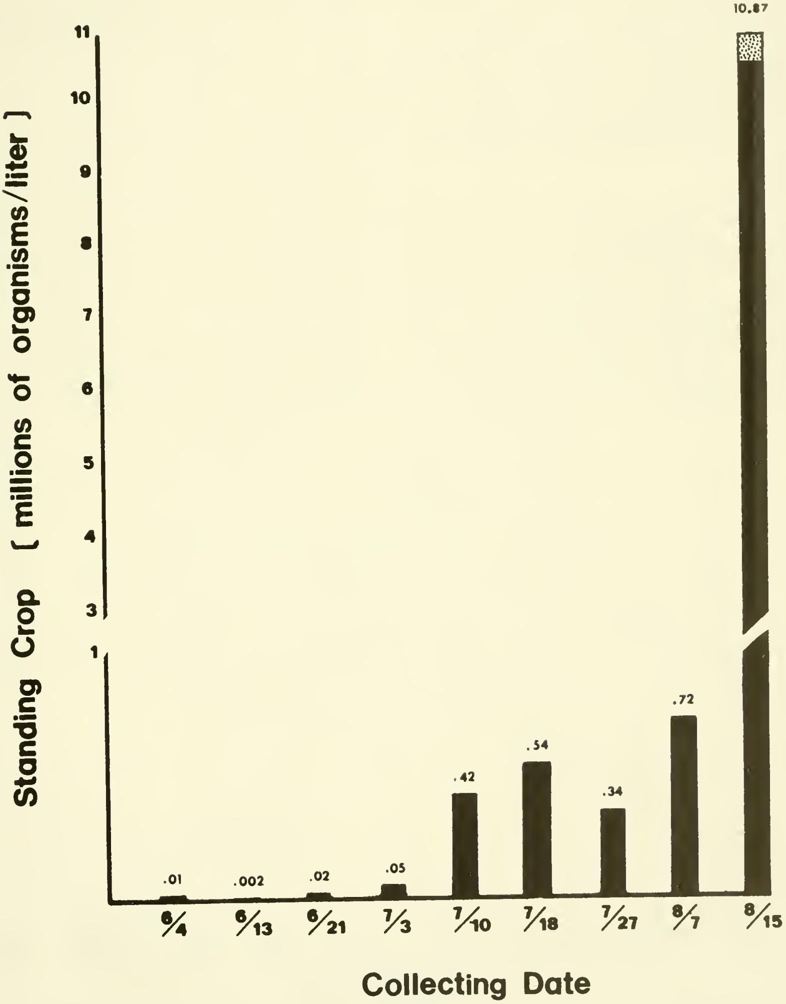

Fig. 3. Mean algal standing crop for collections during the summer of 1974. August 15 sample consisted almost completely of *Aphanizomenon* (solid area) and *Ceratium* (dotted area).

windrows and large amorphous patches. The windrows could possibly be explained by Langmuir circulation currents. The buoyancy of *A. flos-aquae* would cause it to concentrate where converging convection cells cause downwells. The motile *C. hirundinella* may be congregating in the areas of upwelling between the windrows in a manner similar to that reported by George and Edwards (1973) for *Daphnia.* The larger accumulations evident in the lake are more likely due to prevailing winds, which promote horizontal and vertical migrations of algae similar to those reported by Horne and Wrigley (1975) for blue-green algae in Clear Lake, California.

Because *C. hirundinella* is actively motile and *A. flos-aquae* is not, these two algae should respond differently to wind and water currents. Thus, it is possible that the disjunct distribution of these two organisms in Utah Lake is related to a physical parameter.

Because both *Ceratium* and *Aphanizomenon* are apparently well adapted to the environment existing in Utah Lake in August, competition for the resources of space, light, and nutrients could be expected to occur whenever concentrations of organisms become sufficient to deplete these resources. The rapid increase in *A. flos-aquae* standing crop in the second week of August indicated that this alga had greater biotic potential than *C. hirundinella. Aphanizomenon* also may have had a competitive advantage because of its nitrogen-fixing capacity. Thus, when a confrontation occurs between these two organisms, *Aphanizomenon* would be expected to out-compete *Ceratium.*

We conclude that wind and water currents affecting Utah Lake were probable factors in the disjunct distribution of *Aphanizomenon flos-aquae* and *Ceratium hirundinella.* Furthermore, the segregation of these two species may have been augmented by competitive displacement of *Ceratium* by *Aphanizomenon.* The concentration of *A. flos-aquae* into local windrows and amorphous patches, coupled with its removal from other areas, allowed *C. hirundinella* to persist in the lake. The reproductive advan-

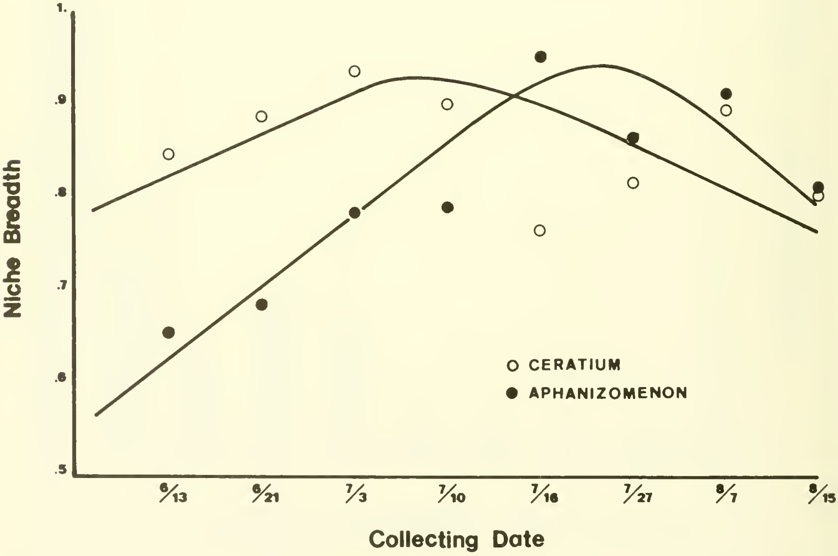

Fig. 4. Niche breadth indices for *Ceratium hirundinella* and *Aphanizomenon flos-aquae* during the summer of 1974.

tage of *A. flos-aquae* may well have resulted in the complete elimination of *C. hirundinella* had it not been for factors preventing its complete occupation of the water column. In the absence of the patchy distribution patterns of the two species, the shift in dominance from *Ceratium* to *Aphanizomenon* would have been attributed inaccurately to seasonal succession.

## ACKNOWLEDGMENTS

We thank K. T. Harper, H. C. Stutz, and J. R. Barnes for their criticism of the manuscript. We acknowledge support from the National Science Foundation and Brigham Young University.

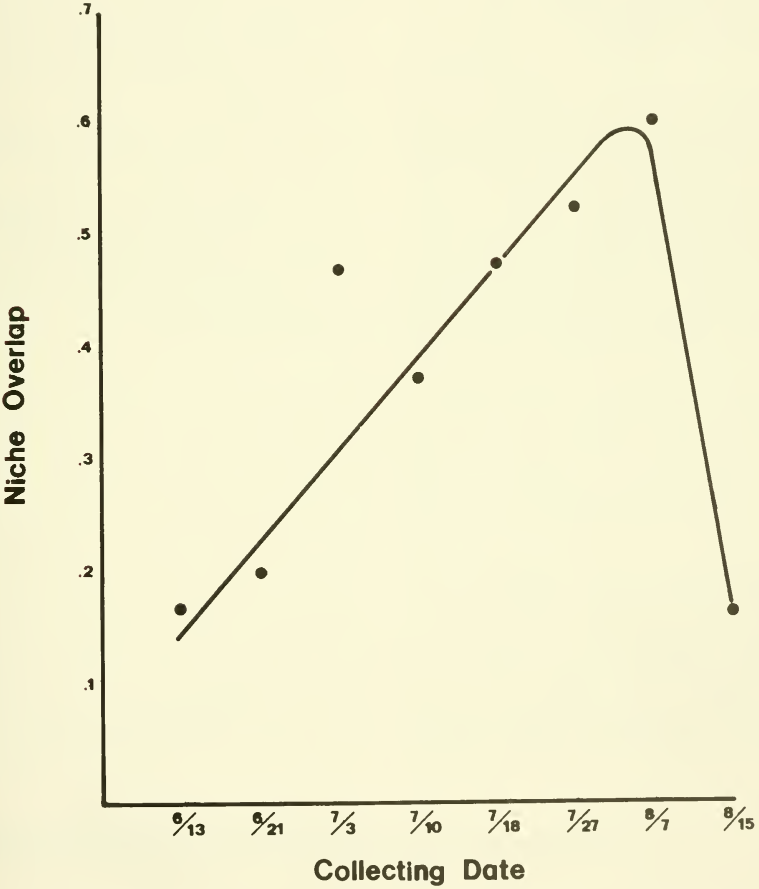

Fig. 5. Niche overlap indices for *Ceratium hirundinella* and *Aphanizomenon flos-aquae* during the summer of 1974.

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# GROUND NESTING AND AGGRESSIVE BEHAVIOR BY THE SWAINSON'S HAWK (*BUTEO SWAINSONI*)

Neil D. Woffinden[1,2] and James A. Mosher[1,3]

ABSTRACT.— A successful ground nesting by Swainson's Hawks, *Buteo swainsoni*, is reported for central Utah. Unusual aggressive nest defense behavior is described for this ground nesting pair.

The Swainson's Hawk (*Buteo swainsoni*) is a large Buteo of western North America, nesting almost exclusively in trees (Bent 1937, Life Histories of North American birds of prey, part 1, U.S. Natl. Mus. Bull. No. 167). In central Utah, on 9 May 1973, we found a Swainson's Hawk nest that was constructed on a rock ledge approximately 1.5 m above the surrounding ground. The ledge sloped gently to the ground providing easy access to the nest. The nearest tree was approximately 700 m to the southwest. The nest was composed primarily of dry sticks, both woody and herbaceous, with green, leaf-bearing branches from juniper (*Juniperus osteosperma*) and atriplex (*Atriplex spp.*). The cup was lined with strips of juniper bark and grass. Three young were successfully fledged from this ground nest.

The nest was used only during the 1973 nesting season. In both 1974 and 1975 Swainson's Hawks successfully nested in the small juniper tree, mentioned above. The tree nest was constructed by refurbishing a Ferruginous Hawk (*Buteo regalis*) nest that had previously been built in the 2 m tree. It is not known if the same pair of hawks were involved in all three nestings; the premise appears likely, however, based on the proximity of the two nest sites. Two young hawks fledged from the tree nest in 1974; one fledged in 1975. It would appear that, because of their greater vulnerability, ground nests would be less productive than tree nests. In this particular case, we feel that any increased vulnerability was compensated by the additional aggressiveness of the ground nesting hawks. However, it should be pointed out that ground nesting Ferruginous Hawks appear to be as reproductively successful as tree nesting pairs.

Bent (1937:231–232) characterized the Swainson's Hawk as "a gentle, unobtrusive bird, living in harmony with its feathered neighbors both large and small." He further stated that this species is not aggressive and "has rarely been known even to threaten to attack an intruder" at the nest. Dunkle (1977, Auk 94:65–71) found Swainson's Hawks nesting in Wyoming to vary in their aggressiveness toward humans, with some females coming to within a few meters of the intruder while others stayed many meters away.

Our nest visits to this Great Basin ground nest elicited highly aggressive behavior from both members of the pair. Attacks were in the form of long, shallow dives that brought the hawks to within a few centimeters of us. These were frequent and intense, and continued until we retreated 30 to 40 m from the nest.

On one occasion, while we were banding the three young, the adults failed to initially react with the usual degree of intensity. A few weak passes were made, after which the female soared to a great height and continued to soar in a tight circle overhead. The male flew from view behind a hill. The female then began a vertical descent, falling rapidly for perhaps 100 m. Pulling out of the

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dive, she circled for a few seconds and began a second descent. At this time the male flew in along the face of the rock outcrop adjacent to the nest ledge, striking the investigator at the nest in the back of the head. Turning 90 degrees, he continued his attack, forcing the second investigator to the ground. He then joined the female who had terminated her dive and was circling above us. They then drifted slowly away from the nest site.

One interpretation of this observation is that nest defense behavior may be a plastic trait and the degree of aggressiveness is related to the security of the nest site. We would encourage others to be alert to this possible relationship between nest defense behavior and nest site security.

We wish to thank J. Edward Gates for reviewing this manuscript. This is Contribution No. 592 Appalachian Environmental Laboratory Center for Environmental and Estuarine Studies, University of Maryland, Frostburg State College Campus, Gunter Hall, Frostburg, Maryland.

# RESPONSE OF REPTILE POPULATIONS TO DIFFERENT LAND MANAGEMENT PRACTICES ON THE IDAHO NATIONAL ENGINEERING LABORATORY SITE

Timothy D. Reynolds[1]

Abstract.— Populations of reptiles were examined in grazed and ungrazed habitats dominated by sagebrush (*Artemisia tridentata*) or by crested wheatgrass (*Agropyron cirstatum*) on the Idaho National Engineering Laboratory (INEL) Site in southeastern Idaho. The sagebrush lizard (*Sceloporus graciosus*) and the short-horned lizard (*Phrynosoma douglassi*) were the only species of reptiles encountered in sufficient numbers to permit statistical analysis. Both of these species preferred sagebrush habitats to areas dominated by crested wheatgrass. The sagebrush lizard was most abundant in the native, ungrazed, sagebrush habitat, and the short-horned lizard was most plentiful in the sheep-grazed area dominated by big sagebrush.

Sagebrush, mostly big sagebrush (*Artemisia tridentata*), was once the dominant vegetation over 100 million ha of western rangelands in the United States (Beetle 1960). In this century, at least 10 percent of the sagebrush range has been altered in an attempt to increase forage production for livestock (Braun et al. 1976). In Idaho, approximately 850 thousand ha of public and private rangeland, most of which was dominated by big sagebrush, have been chemically or mechanically treated and reseeded with crested wheatgrass (*Agropyron cristatum* and *A. desertorum*) (BLM document 1974, L. Sharp, pers. comm.).

With few exceptions, studies concerning the effects of the alteration of sagebrush communities on wildlife have concentrated on game species such as mule deer (*Odocoileus hemionus*), pronghorn antelope (*Antilocapra americana*), elk (*Cervus canadensis*), and Sage Grouse (*Centrocercus urophasianus*) (Patterson 1952, Mackie 1965, Anderson 1969, Peteron 1971). The effects of altering the sagebrush habitat on nongame species have received little attention (Braun et al. 1976).

Reptiles, especially lizards, are important components of North American ecosystems, rivaling mammals and birds with respect to numbers, biomass, and energetics in the desert community (Turner et al. 1976). This vertebrate group is frequently overlooked in environmental studies. The objective of this study was to evaluate the response of reptile populations to different land management practices on the Idaho National Engineering Laboratory (INEL) Site.

## Study Sites

This study was conducted on the INEL National Environmental Research Park Site in southeastern Idaho. The INEL Site occupies 2,315 km$^2$ of cool desert on the Snake River Plain, approximately 48 km west of Idaho Falls, Idaho (Fig. 1). The topography of the site is flat to gently rolling, with frequent lava outcroppings characteristic of the Columbia Plateau Province (Atwood 1970). The elevation ranges from 1454 to 1554 m, with the median about 1500 m. The climate is characterized by hot summers and cold winters, with record high and low temperatures of 39 and −41 C. The mean annual temperature at the Central Facilities Area (CFA) (Fig. 1) is 5.8 C. Precipitation, mostly in the form of spring rains, averages 21.6 cm annually, with a 30-year range of 11.4–36.3 cm. The vegetation of the INEL Site is dominated by big sagebrush (Jeppson and Holte 1976).

Four areas of different land use were selected for study. Two of these were domi-

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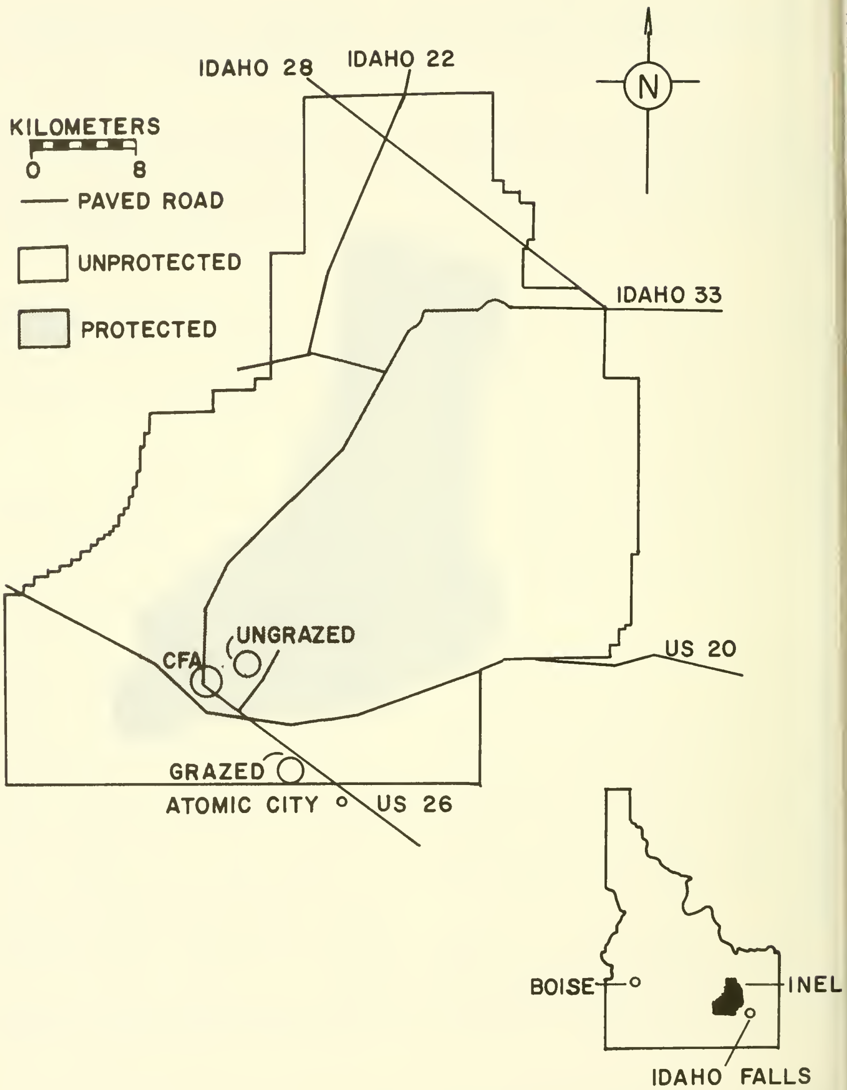
IDAHO 28
IDAHO 22
N
KILOMETERS
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8
PAVED ROAD
UNPROTECTED
PROTECTED
IDAHO 33
US 20
UNGRAZED
CFA
GRAZED
ATOMIC CITY
US 26
BOISE
INEL
IDAHO FALLS

Fig. 1. Location of the grazed and ungrazed study areas on the INEL Site used in determining the response of reptile populations to different land management practices. The grazed and ungrazed sites each contained a habitat dominated by sagebrush (*Artemisia tridentata*) (SAGE) and crested wheatgrass (*Agropyron cristatum*) (CWG). Those portions of the INEL Site protected from livestock grazing are shown.

nated by big sagebrush, and two were former sagebrush range reseeded with crested wheatgrass. One sagebrush and one crested wheatgrass study area were 1.3 km northwest of Atomic City, Idaho, just within the southern boundary of the INEL Site (Fig. 1). The crested wheatgrass here was planted in 1958 or 1959 (INEL Site records vary) after the native vegetation was removed by disking. These two areas were contiguous and have been grazed by 1000–1200 domestic sheep each spring since 1960. These study areas are referred to as grazed sage and grazed CWG.

The other sagebrush and crested wheatgrass study areas were approximately 12 km northwest of the grazed areas (Fig. 1). The sagebrush in this area (ungrazed sage) had received no grazing pressures since 1950, and served as the control plot for this study. The adjacent crested wheatgrass planting (ungrazed CWG) was seeded in 1960, after winter flooding inundated and killed the native vegetation (A. Olson, pers. comm.). Livestock were last permitted in this area 10 years prior to the planting of crested wheatgrass.

## MATERIALS AND METHODS

Vegetation was sampled in each study area along 400 m of line transects with 20 × 50 cm sampling frames (Daubenmire 1959). The percent coverage for each plant species was estimated using six cover classes (0–5, 5–25, 25–50, 50–75, 75–95, and 95–100). The midpoints of each class were used to calculate the average canopy coverage for each species. These values were used in calculating the percent similarity (PS) of the vegetal communities among the study areas (Orloci 1967).

The invertebrate fauna was sampled in an attempt to determine the potential prey available to reptiles in each area of different land use. A 4-ha-square grid was established in each of the study areas, and sweep netting was performed along four transect lines parallel to each axis of the grids. Sweep samples were taken using a standard 38 cm (15 in) canvas sweep net. All transects were swept twice, resulting in 5600 sweeps in each study area.

Pit-fall (sink) traps and a "noose on a stick" (Linder and Fichter 1977) were used to capture lizards. The sink traps were number 10 tin cans buried in the ground at 50 m intervals in a 4-ha grid system, for a total of 25 pitfall traps in each study area. Masonite covers (23 × 23 × 0.5 cm) were placed over the traps when not in use. Initially, these covers were removed for periods not exceeding 4 hours, thus precluding heat prostration of any reptiles in the trap. I found that trapping success was improved and trap mortality reduced to zero when the lids were not totally removed, but propped open slightly with a stick. Thus, the traps were effectively open continuously, but the lids shaded any animals in the trap. Traps were checked at 1- or 2-day intervals from May through October 1977. The noose consisted of a small copper wire or monofilament fishing line fashioned into a slipping noose and attached to the tip portion of a fishing rod. All lizards captured by either method were color-marked with indelible ink for individual identification.

Serpentine species, with the exception of rattlesnakes (*Crotalus viridis*), were hand-captured and color-marked when they were encountered. When a rattlesnake was found, its size was estimated and recorded along with the location of the sighting and any distinguishing characteristics of the snake. The paucity of snakes encountered, and the small number of lizards recaptured, prohibited meaningful estimates of population size by conventional methods. Therefore, the number of reptiles encountered was taken as an indication of the relative density of each species in each of the habitats studied.

## RESULTS AND DISCUSSION

As expected, big sagebrush was the dominant plant species in the sage study areas, and crested wheatgrass was the dominant species on both CWG areas (Table 1). The ungrazed sage had a significantly greater vegetal species diversity (H = 2.85) than did any other area (Table 2). The two CWG study areas exhibited a greater floristic percent similarity (PS = 90 percent) than any other habitat comparisons (Table 2).

Similar numbers of invertebrates were collected in the ungrazed and grazed habitats dominated by sagebrush (181 and 185, respectively) (Table 3). Equal sweep-netting efforts resulted in the capture of approximately 50 percent more invertebrates in each of the crested wheatgrass stands than in either of the sagebrush areas. These differences were significant ($X^2_{.05(1)} = 90.2$).

Four species of reptiles were encountered during the study (Table 4). No serpentine species were found in either of the ungrazed study areas. Gopher snakes (*Pituophis melanoleucus*) and rattlesnakes are generally common and widespread over the INEL Site (Linder and Sehman 1977). The absence of snakes in the ungrazed study areas may not be an accurate indication of the effects of different land use practices on these species. Woodbury et al. (1951), Hirth et al. (1969), and Sehman (1977) recorded maximum dispersal distances of snakes from a hibernaculum of 2.0, 1.3, and 1.9 km, respectively. It is likely that the ungrazed study areas were

TABLE 1. Percent coverage (%) and frequency (f) of plant species in grazed and ungrazed habitats dominated by sagebrush (*Artemisia tridentata*) and by crested wheatgrass (*Agropyron cristatum*) on the INEL Site. Only those species with a frequency of 10 or more, or a percent coverage of at least 1 percent are included.

| | Ungrazed | | | | Grazed | | | |
|---|---|---|---|---|---|---|---|---|
| | Sagebrush | | Crested wheatgrass | | Sagebrush | | Crested wheatgrass | |
| | % | f | % | f | % | f | % | f |
| *Opuntia polyacantha* | 1.3 | 13 | | | | | | |
| *Chenopodium leptophyllum* | 0.6 | 17 | | | | | | |
| *Artemisia tridentata* | 17.00 | 105 | | | 25.00 | 113 | 0.5 | 5 |
| *Aster scopulorum* | 0.7 | 23 | | | | | | |
| *Chrysothamnus nauseosus* | 0.2 | 3 | | | 1.6 | 15 | 0.4 | 5 |
| *Arabis spersiflora* | 0.3 | 11 | 1.0 | 15 | | | | |
| *Agropyron cristatum* | 1.9 | 15 | 52.0 | 160 | | | 39.4 | 154 |
| *Agropyron spicatum* | 6.0 | 35 | | | | | | |
| *Oryzopsis hymenoides* | 5.2 | 34 | 0.2 | 3 | | | | |
| *Poa sanbergii* | 1.8 | 16 | | | | | | |
| *Sitanion hystrix* | 3.0 | 35 | | | 9.2 | 93 | | |
| *Astragalis purshii* | 1.9 | 16 | | | | | | |
| *Phlox hoodii* | | | | | 1.4 | 11 | | |
| *Halogeton glomeratus* | | | | | 1.4 | 4 | 3.9 | 13 |
| Total number of species | 31 | | 3 | | 6 | | 5 | |
| Total percent coverage | 41.6 | | 53.2 | | 38.7 | | 44.1 | |
| Species diversity (H) | 2.85 | | 0.37 | | 1.17 | | 0.54 | |

TABLE 2. Percent similarity (PS) and species diversity (H) comparisons of vegetation in grazed and ungrazed habitats dominated by sagebrush (*Artemisia tridentata*) and by crested wheatgrass (*Agropyron cristatum*) on the INEL Site. Numbers in the upper right portion of the body of the table are PS determinations. Those in the lower left are the results of t-test analysis of species diversity.

| | | Percent similarity | | | |
|---|---|---|---|---|---|
| | | Ungrazed | | Grazed | |
| Diversity | (H) | Sagebrush | Crested wheatgrass | Sagebrush | Crested wheatgrass |
| Ungrazed | | | | | |
| Sagebrush | 2.85 | – | 33 | 38 | 32 |
| Crested wheatgrass | 0.37 | 6.78* | – | 41 | 90 |
| Grazed | | | | | |
| Sagebrush | 1.17 | 20.78* | 2.18* | – | 22 |
| Crested wheatgrass | 0.54 | 8.72* | 0.47 | 2.37* | – |

*H significantly different as $P < 0.05$.

more than 2 km from a suitable denning site. Therefore, snakes were excluded from further analysis.

Two species of lizards were frequently encountered: the short-horned lizard (*Phrynosoma douglassi*) and the sagebrush lizard (*Sceloporus graciosus*). The relative density of both species was significantly greater in each of the sagebrush study areas than in either crested wheatgrass area (Table 5). Significantly more ($X^2_{.05(1)} = 6.92$) sagebrush lizards were encountered in the ungrazed sage than n the grazed sage (Table 5). Conversely, significantly more ($X^2_{.05(1)} = 4.76$) short-horned lizards were found in the grazed sage than in its ungrazed counterpart. The two crested wheatgrass study areas supported populations of both species of lizards that were not statistically different (Table 5).

When the data from the ungrazed sage and ungrazed CWG study areas were combined and compared with the combined data from the two grazed study areas, sagebrush lizards were found to occur significantly more often ($X^2_{.05(1)} = 7.00$) in the absence of grazing. *Phrynosoma douglassi* population levels were not statistically different ($X^2_{.05(1)} = 2.67$) when analyzed in the same manner.

TABLE 3. Number of invertebrates collected in grazed and ungrazed habitas dominated by sagebrush (*Artemisia tridentata*) and crested wheatgrass (*Agropyron cristatum*) on the INEL Site.

| | Ungrazed | | Grazed | |
|---|---|---|---|---|
| Taxon | Sagebrush | Crested wheatgrass | Sagebrush | Crested wheatgrass |
| ARACHNOIDEA | | | | |
| Unclassified | 11 | 6 | 2 | 55 |
| HOMOPTERA | | | | |
| Ceropidae | 3 | 119 | 7 | 8 |
| Ciradellidae | 44 | 7 | 40 | 19 |
| Aphidae | 15 | 0 | 5 | 0 |
| Other | 2 | 1 | 0 | 2 |
| Unclassified | 0 | 0 | 10 | 0 |
| HEMIPTERA | | | | |
| Corizidae | 6 | 0 | 3 | 1 |
| Miridae | 6 | 0 | 12 | 8 |
| Other | 5 | 22 | 1 | 15 |
| Unclassified | 2 | 1 | 2 | 1 |
| COLEOPTERA | | | | |
| Chrysomelidae | 0 | 0 | 0 | 12 |
| Other | 2 | 1 | 5 | 10 |
| Unclassified | 11 | 10 | 12 | 0 |
| ORTHOPTERA | | | | |
| Acrididae | 4 | 13 | 1 | 6 |
| Other | 3 | 3 | 6 | 2 |
| LEPIDOPTERA | | | | |
| Unclassified | 3 | 1 | 5 | 1 |
| DIPTERA | | | | |
| Other | 0 | 0 | 1 | 2 |
| Unclassified | 18 | 25 | 11 | 51 |
| HYMENOPTERA | | | | |
| Formicidae | 27 | 24 | 26 | 23 |
| Other | 0 | 0 | 0 | 7 |
| Unclassified | 19 | 37 | 36 | 53 |
| TOTAL | 181 | 270 | 185 | 276 |

## CONCLUSIONS

Populations of lizards responded differently to different land management practices on the INEL Site. Grazing by sheep in a habitat dominated by sagebrush resulted in a significant reduction in the plant diversity of that area. This was not accompanied by a concommitant change in the relative density of either the invertebrate or reptilian fauna. Planting a former sagebrush range with crested wheatgrass resulted in a further re-

TABLE 4. Number of reptiles encountered in grazed and ungrazed habitats dominated by sagebrush (*Artemisia tridentata*) and by crested wheatgrass (*Argopyron cristatum*) on the INEL Site.

| | Number encountered | | | |
|---|---|---|---|---|
| | Ungrazed | | Grazed | |
| Taxon | Sagebrush | Crested wheatgrass | Sagebrush | Crested wheatgrass |
| Short-horned lizard (*Phyronosoma douglassi*) | 17 | 4 | 26 | 7 |
| Sagebrush lizard (*Sceloporus graciosus*) | 37 | 5 | 21 | 0 |
| Gopher snake (*Pituophis melanoleucus*) | 0 | 0 | 2 | 0 |
| Great Basin rattlesnake (*Crotalus viridis*) | 0 | 0 | 3 | 3 |

TABLE 5. Results of chi square analysis of the number (N) of sagebrush lizards (*Sceloporus graciosus*) and short-horned lizards (*Phrynosoma douglassi*) encountered in grazed and ungrazed habitats dominated by sagebrush (*Artemisia tridentata*) and by crested wheatgrass (*Argopyron cristatum*) on the INEL Site.

| | | Study area | | | |
|---|---|---|---|---|---|
| | | Ungrazed | | Grazed | |
| Species and number encountered | N | Sagebrush | Crested wheatgrass | Sagebrush | Crested wheatgrass |
| Short-horned lizard (*Phryonosoma douglassi*) | | | | | |
| Ungrazed | | | | | |
| Sagebrush | (17) | – | 9.94* | 4.76* | 5.88* |
| Crested wheatgrass | (4) | | – | 16.13* | 0.82 |
| Grazed | | | | | |
| Sagebrush | (26) | | | – | 10.94* |
| Crested wheatgrass | (7) | | | | – |
| Sagebrush lizard (*Sceloporus graciosus*) | | | | | |
| Ungrazed | | | | | |
| Sagebrush | (37) | – | 27.68* | 6.92* | 36.01* |
| Crested wheatgrass | (5) | | – | 9.58* | 3.20 |
| Grazed | | | | | |
| Sagebrush | (21) | | | – | 19.05* |
| Crested wheatgrass | (0) | | | | – |

*Significant at $P < 0.05$.

duction in the diversity of vegetation. This was accompanied by an apparent increase in the relative density of invertebrate fauna (especially arachnids, dipterans, and hymenopterans), although the populations of lizards were significantly below that found in the sagebrush habitats. The increase in invertebrates in the crested wheatgrass plantings may indeed be a very real phenomena, or it may indicate a shortcoming in using sweep-nets as a sampling technique in habitats that are structurally different.

Ants are the primary prey items of both the sagebrush lizard (Burkholder and Tanner 1974) and the short-horned lizard (Guyer 1978), and it is interesting to note that formicids were in equal abundance in each of the four habitats studied (Table 3). Thus, if prey alone was the factor controlling the distribution of lizards, one would expect equal densities of lizards in each of the four habitats of different land use. This, of course, was not the case, indicating that the physiognomy of the vegetation, as well as the presence of potential prey, is vital in determining the density of saurians, and most likely reflects the coevolution of these lizard species with the sagebrush environment.

Grazing a sagebrush habitat appeared to improve that habitat for *P. douglassi*, whereas S. *graciosus* population levels seemed to be lowered by livestock grazing. The mechanism(s) responsible for this disparity in the response of these species to grazing practices is not known. It is possible that the few forbs and grasses in the grazed sage study area (Table 1) resulted in more, or improved, basking sites for the short-horned lizard, but the lack of ground cover had a negative effect on the sagebrush lizard populations. The precise microhabitat affinities of these lizards are not recorded in the literature. Thus, the results presented here may reflect abiotic and biotic differences, as yet undetermined, among the four habitats studied. In any case, converting a sagebrush range to crested wheatgrass resulted in the reduction of the population levels of both the short-horned and sagebrush lizards. And, once the native vegetation was replaced by crested wheatgrass, grazing did not appear to further affect the lizard populations.

As the production of agricultural products increases to keep pace with the ever increasing demand for red meat protein, it is likely that more and more acreage of habitat dominated by sagebrush will be converted to monocultures of crested wheatgrass. Additionally, efforts to reclaim strip-mined lands in the Intermountain West rely heavily on the planting of crested wheatgrass for initial soil stabilization. Thus, crested wheatgrass plantings are becoming more widespread in our environment. This study, and others like it (Reynolds 1978), indicate that the continued conversion of habitats dominated by sagebrush to large expanses of crested wheatgrass will have a long-term and deleterious effect on the populations of native vertebrates.

## Acknowledgments

I thank C. Guyer, M. Mahoney, and M. Reynolds for assistance in installing and regularly monitoring the sink traps. S. Condie and J. Jensen provided invaluable assistance in the collection and classification of the invertebrate fauna. Drs. J. E. Anderson, E. Fichter, O. D. Markham, and C. H. Trost critically evaluated an earlier draft of the manuscript. J. and G. Millard offered useful suggestions. This is a contribution from the INEL Site Radioecology-Ecology Studies Program, administered by the U.S. Department of Energy.

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# DECREASES OF JUNIPER WOODLAND IN THE UTAH AND SALT LAKE VALLEYS SINCE SETTLEMENT

E. M. Christensen[1] and J. D. Brotherson[2]

ABSTRACT.— Although pinyon-juniper woodland is common throughout most of Utah, it is less so in Utah and Salt Lake valleys. Even so, stands do occur in the valleys and are known to have been there since presettlement times. Three such stands occurring along the eastern sections of the valleys have shown major decreases in area since settlement times, and one has all but disappeared. Their disappearance is attributed to early use for fuel, agricultural, and urbanization purposes.

The expansion since pioneer days of pinyon-juniper woodland in the foothills and benchlands of Utah is a well-known and documented phenomenon. Parker (1971) and Barney (1972) summarized the literature concerning the invasion of pinyon-juniper woodland that was earlier described by Mason (1963) as taking place on deep soils, relatively free of stones, and which formerly "supported a dense cover of grass, forbs, and shrubs."

In the eastern part of the Salt Lake and Utah valleys, however, an opposite trend has occurred: a decrease of junipers and juniper woodland.

Discussed here are decreases in three established stands of juniper as described by early pioneer residents. Pinyon pine (*Pinus edulis* Englem.) does not occur in Salt Lake Valley and is rare in Utah Valley (Erdman 1970). Therefore, the woodlands here described are essentially composed of Utah junipers (*Juniperus osteosperma* (Torr. Little), also known locally as "cedar."

## HISTORICAL DISTRIBUTION OF JUNIPER

It is generally believed that at the time of settlement, the Salt Lake Valley had few native trees on the foothills and benchlands (Smith 1953, Roberts 1965), although trees are known to have been common along the streams (Wakefield 1933, Wakefield 1936). Part of Salt Lake City's folklore indicates that there was only one tree in the valley, a Utah juniper located at 300 South and 600 East Streets (Young 1930, Carter 1940), although other trees were noted by Brigham Young in 1847 (Young 1930). The stump of this particular tree stood for many years after the tree died in 1933 and part of it is still preserved under a monument canopy. Junipers were apparently not abundant in the Salt Lake Valley at the time of settlement because most early descriptions found in diaries and reports do not mention them (Wakefield 1933, 1936). There were some junipers scattered throughout the valley, however, as is shown in the writings of Langworthy (1855), Bryant (1949), and Gunnison (1852). Langworthy observed Salt Lake Valley from the southeast on 11 July 1850. He was impressed by the scarcity of trees, but noted the conifers on the hillsides:

> . . . The whole expanse looks bleak and naked, there being no trees in sight except a very few along the banks of streams, and some stunted, scattering pines and cedars on the sides of the mountains.

Bryant, traveling through the Salt Lake Valley in 1849, also recorded the occurrence of junipers on the sides of the mountains:

> . . . Hidden away in the profound chasms and along the streams whose beds are deeply worn in the mountain sides are the cedar, pine, dwarf-maple, and occasionally oak, where the inhabitants of the vale seek their fuel and building timber . . .

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The situation in Utah Valley was much the same as that in Salt Lake Valley. Cottam, the first ecologist to describe the vegetation in Utah Valley, commented that on the "western escarpment of the Wasatch . . . except for white fir near the summit, the absence of trees is noticeable" (Cottom 1926). Carvalho, who saw Utah Valley some 70 years earlier on 6 May 1854 (Carvalho 1860) stated:

> . . . The scenery, which is enlivened by . . . flowering vales . . . is without timber except on the creeks which meander from the mountains . . . Sparse growths of young cottonwood are the only trees I have seen except in the cannons of the mountains, on which grow pines, cedars, and a species of mahogany.

Huntington (1842), an early pioneer, described Utah Valley in 1849 in his diary:

> . . . Besides the Salt Lake Valley are several smaller valleys, the largest of which is the Ewtah, which would be the end of my searches to find a pleasant and delightful home . . . The most of the western side of the valley is . . . covered with juniper trees . . . the borders of . . . creeks and rivers are well stocked with wood.

There are juniper stands with old trees on the hillsides near the mouths of several canyons in both valleys: Parley's Canyon, Mill Creek Canyon, Tolcat's Canyon, Big Cottonwood Canyon, Spanish Fork Canyon. These groves are rather open and the older trees are usually highlined from browsing. There is little reproduction in the stands, but it appears sufficient to maintain the present density of the existing stands. These juniper stands were doubtless present in pioneer days, and are the types of stands referred to in the descriptions given above.

## Decrease of Presettlement Juniper Stands

Point of the Mountain Stand.— There were several well-established juniper stands of various sizes in Salt Lake and Utah valleys when settlement began. One of these was at Point of the Mountain near Jordan Narrows on the Traverse Range (T4S, R1W, S 13, 23, 24). The stand was generally ignored in the descriptions of the early travelers and pioneers, probably because the road bypassed it. This stand was still present in 1933 when Wakefield studied the ecology of early Salt Lake and Utah valleys (Wakefield 1933), but Wakefield did not note its size. Prior to the development of the gravel pits and the construction of Interstate Highway I-15 during the past 15 years, there was an open grove of juniper trees remaining on the hill east of the road. Presently, there are only about 20 to 30 trees, which are scattered along the tops of the road cut of the I-15 Highway and the adjacent gravel pits to the north.

Another remnant stand of junipers also exists a few miles northeast of Lehi at Cedar Hollow, located about half a mile east of Lehi Cemetery (T5S, R1E, S3,4). The history of the community is unknown to the authors, but there are a few juniper trees there at the present time.

Mapleton Stand.— In 1926 Cottam described only one stand of junipers in eastern Utah Valley (which is an indication that it was the largest one in the valley). He observed:

> . . . the juniper belongs largely to the mountains. It is found sparingly on Mapleton Bench, but it reaches association rank on the slopes of Lake and West mountains.

By "association rank" Cottam meant that the species was a dominant of a major plant community. Lake and West mountains are on the western boundary of Utah Lake. By 1933 Wakefield noted "but a few remnant areas [of juniper communities] on Mapleton Bench."

Observations of early pioneers give the impression that in presettlement times this juniper stand was more extensive than either the brief descriptions of Cottam or Wakefield indicate. Mae B. Huntington summarized the impressions of the first pioneers of the Springville area with considerable emphasis on vegetation (Huff 1947):

> When the Pioneers alighted from their wagons that September afternoon in 1850, one pioneer mother said it looked like a heaven on earth. The weary travelers stood knee-deep in native grass. They saw the benchlands nearby covered with cedars. They saw the distant hills covered with cottonwood and balsam.

In a history of Springville, Johnson (1900) relates an incident of the O. B. Huntington party in February 1849, when the horses strayed one night from a campsite in Springville toward the mouth of Maple Canyon "through the cedars which grew on what is now known as Mapleton Bench."

Much of Springville and Mapleton occupy the original area that supported junipers, but today only a remnant of the grove (mostly south of Evergreen Cemetery, T8S, R3E, S9) remains to remind us of the stand that the pioneers knew.

Manila Stand.— This stand is located about 1.5 miles north of Manila and about a mile east of the Alpine Country Club (T4S, R2E, S31; T5S, R2E, S6). It is restricted to a west-facing slope (approximately 25 degrees) south of American Fork Canyon and west of Highway 146. Although it was not mentioned by Cottam or Wakefield, the stand was evidently present when settlement occurred. A ring count on one medium-sized tree (2.8 dm. diameter at 1 foot above the surface) indicated that the tree was over 190 years old in 1963. The stand was apparently rather large at one time. On 15 December 1850, George A. Smith was in a grove of junipers located between American Fork and Provo, where he "found about 50 wagons camped in the cedars." He may have been referring to the Manila Stand. If so, the grove must have been larger than it is today to have accommodated 50 wagons, and it must have extended onto the surrounding level ground. If Smith was in another stand of junipers, it has completely disappeared because no other groves of junipers exist between the two cities today. In either case, a decrease of juniper woodland is indicated.

In 1849, a group of 50 men led by Parley P. Pratt may have camped in this same grove of junipers. Colton (1946) gave the account of Robert T. Campbell, the clerk of the company who wrote on 25 November 1849:

> The company traveled to Cedar Grove where they camped at 4 or 5 p.m. about two and one-half miles from the Utah Fort.

Two days later they reached Provo River. It is about 12 miles from the Manila Stand to the site of Utah Fort and about 9 miles to the mouth of Provo Canyon, so either Campbell's estimation of distance was poor, the grove was much larger than today, or the group was in another "Cedar Grove" nearer to Provo that no longer exists.

In 1963 E. M. Christensen studied the Manila Grove. It was then about one mile long and one-quarter of a mile wide. Today it covers less than one-third of the area it covered in 1963, having been reduced primarily by gravel mining, road building, and a tract housing development. In 1963, there were 90 juniper trees per hectare (stems 1 dm in diameter at 1 foot above surface and larger) and 21 juniper plants per hectare smaller than tree size. The projected foliar cover of the ground surface of the junipers was 11 percent. The average diameter of the trees was 2.4 dm (9.4 inches at 1 foot above the ground. The stand has been heavily grazed, gully errosion is evident, and exotic species are common in the understory. With the present housing development under construction, this stand will most likely disappear within the next 10 to 15 years.

## Summary

A conclusion can be made that there were juniper woodland stands in the eastern sections of Salt Lake and Utah valleys at the time of settlement by white men. Decrease in the area occupied by at least three of these juniper groves has occurred, even though increases in juniper have occurred elsewhere in Utah. In addition, juniper trees were scattered throughout these valleys, and, doubtless, the number of such trees has also decreased. Urbanization, agriculture, fuel procurement, etc., appear to be responsible for at least some of the decrease.

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# COMPETITION BETWEEN HARVESTER ANTS AND RODENTS IN THE COLD DESERT[1]

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Abstract.— Local distribution patterns of three rodent species (*Perognathus parvus, Peromyscus maniculatus, Reithrodontomys megalotis*) were studied in areas of high and low densities of harvester ants (*Pogonomyrmex owyheei*) in Raft River Valley, Idaho. Numbers of rodents were greatest in areas of high ant-density during May, but partially reduced in August; whereas, the trend was reversed in areas of low ant-density. Seed abundance was probably not the factor limiting changes in rodent populations, because seed densities of annual plants were always greater in areas of high ant-density. Differences in seasonal population distributions of rodents between areas of high and low ant-densities were probably due to interactions of seed availability, rodent energetics, and predation.

Competition for food is an important determinant of ecosystem structure and dynamics (Hairston et al. 1960, Brown and Davidson 1977), but, because the relative importance of competition as a determinant of community composition is debatable (Schoener 1974, Wiens 1977), additional study is essential to provide necessary insights into community relationships. Most studies of competition have dealt with interactions between species of closely related taxa (Connell 1961, Brown 1971, Sheppard 1971, Grant 1972, MacArthur 1972, Pianka 1974, Schroder and Rosenzweig 1975), but only recently have they included species of more distantly related taxa (Hansen and Ueckert 1970, Brown et al. 1975, Fenton and Fleming 1975, Primack and Howe 1975, Pulliam and Brand 1975, Sinclair 1975, Brown and Davidson 1977, Boyden 1978).

Although studies of harvester ants in North America have included distribution (Hull and Killough 1951, Sharp and Barr 1960, Cole 1968), damage and control (Cole 1932, Severin 1955, Lavigne 1966, Race 1966, Wight and Nicholes 1966), foraging activity (Cole 1934, Creighton 1953, Tevis 1958, Bernstein 1974, Rogers 1974, Whitford and Ettershank 1975, Whitford 1976), species diversity (Davidson 1977a, 1977b, Mares and Rosenzweig 1978), and taxonomy (Cole 1968), only a few studies in Arizona have examined competition between ants and rodents (Brown et al. 1975, Pulliam and Brand 1975, Brown and Davidson 1977, Reichman, unpubl. ms.). Reichman (unpubl. ms) demonstrated that either taxon alone or both together impact the density of seeds in the soil, but Pulliam and Brand (1975) concluded that little competition exists between ants and rodents except in years of low seed production. Brown and Davidson (1977) concluded that ants and rodents do compete for seeds in southern hot deserts, and harvester ants can affect rodent distribution.

Our objective was to investigate local distribution patterns of rodents and ants to determine if competition for seeds was an important factor in any observed interaction between western harvester ants and rodents in the cold desert.

## Study Sites and Methods

This study was conducted in a sagebrush-greasewood community at Raft River Valley, Idaho, from May through August 1977 and 1978. Predominant plant species were sagebrush (*Artemisia tridentata*), greasewood (*Sarcobatus vermiculatus*), squirreltail barley (*Sitanion hystrix*), and mustards (*Lepidium perfoliatum* and *Descurainia richardsonii*). Harvester ants were of the species *Pogono-*

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[1] This research was sponsored by EG & G, Idaho, Inc., and supported by the U.S. Department of Energy Contract DE-A507-77ID01674.

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*myrmex owyheei.* Rodent species investigated were the white-footed deer mouse (*Peromyscus maniculatus*), western harvest mouse (*Reithrodontomys megalotis*), and Great Basin pocket mouse (*Perognathus parvus*).

One 12 × 12 base grid with 15 m between stations, and 10 4 × 5 mini-grids with 10 m between stations were established to assess ant-rodent interactions. Approximately half of the base grid and five of the mini-grid were located in areas of high ant-density, but the remainder of the base grid and the other five mini-grids supported only low ant-densities.

Two Utah live traps (Garcia et al. 1974) baited with rolled oats were placed at each station on the base grid, which was trapped for 10 consecutive nights during May and August 1977 and 1978. The 10 mini-grids, with one Utah live trap at each station, were trapped simultaneously for four consecutive nights each month. Mini-grids were trapped prior to the base grid trapping in May and August. All animals on the base grid and mini-grids were marked for identification by clipping the toes and released after species, sex, and trap station were recorded. Numbers of rodents for the mini-grids and centers of activity on the base grid were estimated using Hayne's (1949a, 1949b) methods.

Understory vegetation (<30.5 cm high) and overstory vegetation (>30.5 cm high) were measured using the cover class and point quarter methods, respectively. Relative seed abundance and time of seed drop of annual forbes (*Descurainia richardsonii, Lepidium perfoliatum*) and grass (*Sitanion hystrix*) was determined monthly on the 10 mini-grids from soil samples, using the method of Franz et al. (1973).

In order to establish a relationship between distribution of *P. maniculatus* and seed abundance during the May reproductive period, sex ratios were calculated for specimens collected from the 10 mini-grids.

Ant mound volumes were used in conjunction with numbers of mounds per unit area to estimate ant density at each mini-grid (Fig. 1). Ant foraging activity was estimated twice each day during the first week of each month by placing a one-meter quadrat over each of 22 stations located 15 m apart in the area of high ant-density of the main grid. Numbers of active ants/m$^2$/minute were counted and averaged to obtain a monthly estimate of relative foraging activity. Seed preferences of harvester ants were determined on 23 June and 6 and 28 July 1978 for five mounds. Seeds were collected, identified, and counted from 75 returning foragers for each mound at each sampling period.

## RESULTS

Areas of high ant-density had less total cover (32.8 percent and 42.2 percent in high and low ant-density areas, respectively) and less grass cover (0 and 32.7 percent in high and low ant-density areas, respectively) than did areas of low ant-density. Densities of seeds from annual plants (*Descurainia richardsonii, Lepidium perfoliatum*) were apparently dropped in late May and early June, whereas *Sitanion hystrix* seeds were dropped in July and August (Table 1). This temporal difference in seed drop was also reflected by the foraging activities of the ants (Table 2). In June, ants almost exclusively foraged on seeds from *D. richardsonii* and *L. perfoliatum,* whereas in July they foraged on *S. hystrix* (Table 2).

Ant foraging activity was lowest in May, peaked in July, and decreased in August (Table 3). There was a significant negative correlation ($p<0.025$) between ant densities and rodent numbers (Fig. 2), but no significant correlation between rodent numbers and seed abundance ($p<0.200$).

Average numbers of rodents in areas of low ant-density were 9 ± 3.2 rodents/grid in May and 16 ± 2.7 in August, an 88 percent increase; in areas of high ant-density the numbers of rodents were 26 ± 8.3 in May and 11 ± 2.7 in August, a 58 percent decrease (Table 4). Centers of rodent activity on the base grid shifted from the area of high ant-density to the area of low ant-density during August 1977 and 1978 (Table 4).

Sex ratios of *P. maniculatus* during the May reproductive period on the five mini-grids with low seed-density averaged 1.6:1 (1:1 to 2:1) males to females, and on the five grids with high seed-density they averaged 1:1.3 (5:11 to 13:8). When fitted to a binomial distribution these ratios were significantly different ($p<0.08$) in both high and low seed-density areas. The female-to-male sex ratios were also significantly greater ($p<0.04$) in the areas of high seed-densities.

## DISCUSSION

Studies of competition by Brown and Davidson (1977) between ants and rodents in Arizona indicate that seeds limit the distribution of either taxon, which also influences each other. Although they demonstrated significant evidence for exploitation competition between ants and rodents, our data from Idaho show that factors other than seed abundance are more influential in changing rodent distributions in areas of high ant-density. Our data indicate that *D. richardsonii* and *L. perfoliatum* seeds were always more abundant in areas of high ant-densities than they were in areas of low ant-densities (Table 1). Because this condition persisted in spite of greater foraging pressure by ants and rodents, these seeds probably did not limit rodent populations or distribution. If seed of these species were not the limiting factor, then rodent populations should not have declined by 58 percent in areas of high ant-density. One might suspect an error in our data due to inappropriate sampling, but comparable results were obtained on the base grid. In August 1977 and 1978, significant shifts occurred in the centers of activity from the area of high ant-density to the area of low ant-density (Table 4). In fact, two *P. maniculatus* that established centers of activity in the area of high ant-density during May established new centers of activity in the area of low ant-density during August.

The negative correlation between ants and

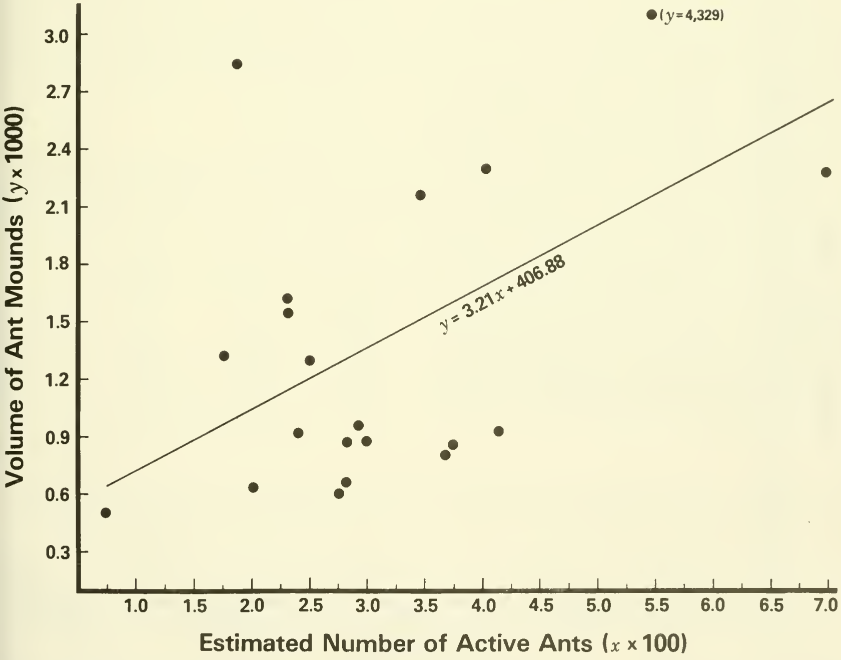

Fig. 1. Regression analysis of mound volume and estimated number of active ants ($p<0.050$).

TABLE 1. Relative seed abundance and time of seed drop for *Descurainia richardsonii*, *Lepidium perfoliatum*, and *Sitanion hystrix* for May–August 1977.

| | Annual seeds per sample | | | Grass seeds per sample | | |
|---|---|---|---|---|---|---|
| Date | High ant-density | Low ant-density | Average | High ant-density | Low ant-density | Average |
| May | 128 | 25 | 77 | 0 | 27 | 14 |
| June | 242 | 53 | 147 | 4 | 31 | 18 |
| July | 199 | 126 | 163 | 2 | 86 | 44 |
| August | 144 | 16 | 81 | 0 | 78 | 39 |
| Average | 179 | 55 | | 3 | 56 | |

TABLE 2. Numbers and relative percentage of seeds from *Descurainia richardsonii*, *Lepidium perfoliatum* and *Sitanion hystrix* (grass) collected from 75 foraging ants at five ant mounds for the four sampling periods in 1978.

| | | | | Percent of total | |
|---|---|---|---|---|---|
| Date | Annual seeds | Grass seeds | Number combined | Annual seeds | Grass seeds |
| June 23 | 358 | 1 | 359 | 99.7 | 0.3 |
| July 6 | 249 | 16 | 265 | 94.0 | 6.0 |
| July 16 | 47 | 88 | 135 | 35.0 | 65.0 |
| July 28 | 39 | 111 | 150 | 26.0 | 74.0 |

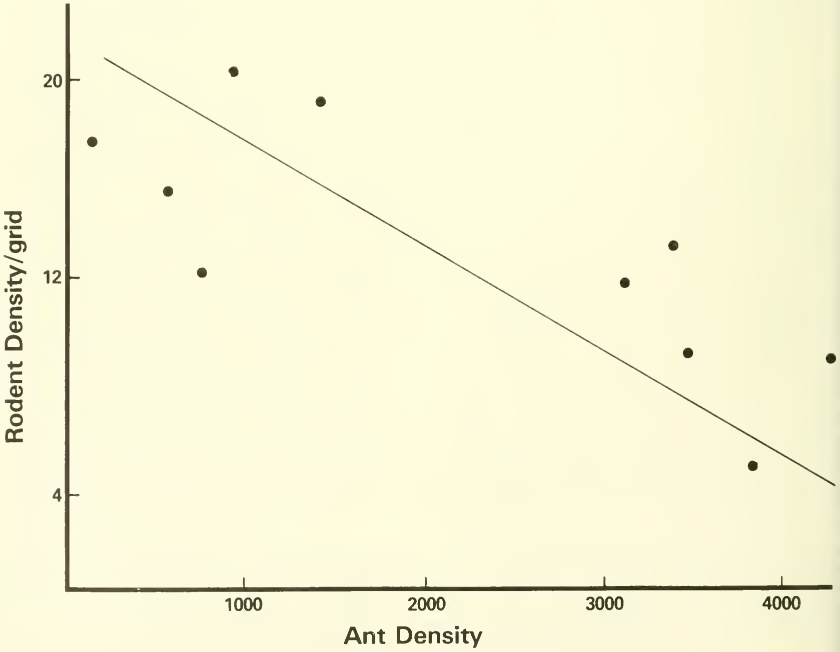

Fig. 2. The correlation between ant and rodent density ($p<0.025$) is shown for May–August 1978.

rodents (Fig. 2), the 58 percent rodent population decline in areas of high ant-density (Table 3), and the shifts in rodent centers of activity (Table 4) indicate that interactions did occur between ants and rodents. Competition for seeds is probably not responsible for these interactions; consequently, other factors such as rodent energetics, predation, and seed availability may logically be expected to account for rodent distribution changes in areas of high ant-density. During the critical reproductive period in May, female rodents must secure sufficient energy for existence and successful rearing of young. At that time it seems critical that females be in areas of relatively high food abundance in order to maximize reproductive energy. Assuming this to be the case, two predictions can be generated: (1) rodent numbers will be higher in areas where seed abundance is greatest and (2) sex ratios will be weighted toward females in areas of high seed-density. Both of these predictions were realized in our studies. Areas of high seed-density were also the areas of highest ant densities (Table 1), but, because ants were inactive in May (Table 3), competition between ants and rodents for seeds was nonexistent at that time.

Because of the temporal difference in seed drop between the annual herbaceous species (*D. richardsonii, L. perfoliatum*) and grass (*S. hystrix*), seeds from annual plants are more available in May and June, whereas the grass seeds are more available in July and August. This difference in seed availability was also reflected in the foraging activities of harvester ants. They foraged almost entirely on seeds from annual plants in June, but, as the season progressed and these seeds became less available due to ant-rodent foraging activities and the loss of seeds into soil crevices (Tevis 1958, Bernstein 1974), ants foraged primarily on grass seeds that were more available (Table 2). Since grasses were virtually nonexistent in areas of high ant-density (Table 1), rodents likely emmigrated to areas where those seeds were more abundant.

Rodents living in areas of high ant-density would probably be more susceptible to predators than those living in areas of low ant-density for two reasons: (1) areas of high ant-density have more open spaces and less total cover than areas of low ant-density (Table 1), (2) foraging time will increase as the seed availability of *D. richardsonii* and *L. perfoliatum* decrease. Observations in July and August indicated that predator pressure on rodents was greater in areas of high ant-density. Short-eared owls and burrowing owls were observed almost exclusively in those areas. Coyote signs were more abundant in areas of high ant-density, and the only weasel captured during the summer was on a grid with high ant-density. Because ecological theory suggests that small animals are more likely to be regulated by predation than competition (Hairston et al. 1960, Schoener 1974), our results suggest an alternative ex-

TABLE 3. Mean numbers ± standard deviation or rodents/grid in areas of high and low ant-densities, and the relative ant-foraging activity for the period May–August 1978.

| | Mean no. rodents/grid | | |
|---|---|---|---|
| Date | High ant-density area | Low ant-density area | Relative foraging activity |
| May | 26 ± 8.3 | 9 ± 3.2 | 8 ± 12 |
| June | 29 ± 6.2 | 24 ± 4.3 | 56 ± 30 |
| July | 17 ± 4.1 | 18 ± 2.8 | 104 ± 70 |
| August | 11 ± 2.7 | 16 ± 2.7 | 26 ± 13 |

TABLE 4. Distribution of centers of rodent activity for areas of high and low ant-densities on the base grid for May and August 1977 and 1978.

| Rodent centers of activity | May | | | August | | |
|---|---|---|---|---|---|---|
| | High ant-density area | Low ant-density area | Total | High ant-density area | Low ant-density area | Total |
| Number, 1977 | 16 | 27 | 43 | 3 | 12 | 15 |
| Number, 1978 | 31 | 34 | 65 | 16 | 29 | 45 |
| Percentage, 1977 | 37 | 63 | | 20 | 80 | |
| Percentage, 1978 | 48 | 52 | | 35 | 65 | |

planation for observed ant-rodent distribution patterns to that proposed by Brown and Davidson (1977).

Differential predation pressure and seed availability are factors that have not been treated as complimentary mechanisms influencing rodent distributions in areas of high ant-density. Although this is the first reported study of ant-rodent interactions in a cold desert, the results suggest that competition for seeds between the two taxa may not be as intense in cold deserts as indicated by Brown et al. (1975), Brown and Davidson (1977), and Reichman (unpubl. ms.) for the Sonoran Desert. Pulliam and Brand (1975) reported that competition for seeds between ants and rodents in the plains grassland region of Arizona may occur only in periods of drought. Because 1978 was an exceptional year for production of annuals (19.2 percent relative cover compared to 6.8 percent in 1977), active competition for seeds between the two taxa may have been masked.

Ants may exert a stronger influence on rodent distributions in cold desert environments than our data have shown. Because ants have an impact on the total vegetation cover of an area (Rogers and Lavigne 1974, Clark and Comanor 1975), their absence may allow increases in total shrub and grass cover, thus affecting rodent distributions. The decrease in availability of seed from annual plants probably would not be as dramatic if there were no ants present. If this were the case, then foraging time and consequent predation would not increase significantly as the season progressed. Further documentation of selection pressures such as predation and seed availability during drought years are needed before the extent of competition between ants and rodents in cold desert environments can be fully evaluated.

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# FOOD HABITS OF BURROWING OWLS IN SOUTHEASTERN IDAHO

R. L. Gleason[1] and T. H. Craig[2]

ABSTRACT.— Food habits of a population of the Burrowing Owl (*Athene cunicularia*) at the Idaho National Engineering Laboratory, Butte County, were studied. The 421 pellets examined yielded 2,436 prey items of at least 22 prey species. Invertebrates, largely insects, constituted 91 percent of the total prey items, but only 29 percent of the total biomass; mammals constituted 8 percent of the prey items, but 68 percent of the biomass. The prey were mostly nocturnal species; diurnal species were poorly represented.

The Burrowing Owl (*Athene cunicularia*) is widely distributed in the dry prairies and grasslands of western North America. In Idaho, Burrowing Owls are breeding residents on the Snake River Plains, generally arriving in April and departing in October. Although the food habits of Burrowing Owls have been documented in much of their range (Robertson 1929, Errington and Bennett 1935, Hamilton 1941, Sperry 1941, Bond 1942, Longhurst 1942, Thomsen 1971, Butts 1973, Marti 1974), including Oregon (Maser et al. 1971) and Utah (Smith and Murphy 1973a), this paper provides the first information from Idaho.

The study population was located within and adjacent to the 2315 km$^2$ Idaho National Engineering Laboratory (INEL) Site in Butte Co. Elevation on the INEL Site ranges from 1454 m to 1554 m. Rainfall averages less than 25 cm a year, with large annual variations. The average monthly temperatures are below 0 C for November through March, and approach 20 C for the hottest month, July. Vegetation is dominated by big sagebrush (*Artemisia tridentata*), which covers about 80 percent of the site (Harniss and West 1973).

Pellets were collected at nine active burrows from 4 June to 29 July 1975. This was approximately the period from hatching of the young to dispersal of the family groups. Burrows were visited about every four days and pellets were usually found within a radius of several meters from the burrow entrances. Pellets were dissected in the laboratory and the number and identity of prey remains in each pellet were recorded. Mammalian remains were identified by dental characteristics, and mandibles were paired to determine the total number of individuals represented. Invertebrate prey were identified and counted using recovered mandibles, heads, and/or elytra. Average body weights were taken from Smith and Murphy (1973b), Evans and Emlen (1974), Johnson (1977), and Diller (pers. comm.).

A total of 421 pellets yielded 2,436 prey items and indicated that the owls utilized at least 22 species of prey (Table 1). Invertebrates were the most frequent prey of Burrowing Owls on the INEL Site, constituting about 91 percent of the total number of prey items. However, invertebrates represented only 29 percent of the total biomass. Conversely, mammals represented 8 percent of the total prey items, and 68 percent of the total biomass. Similarly, Smith and Murphy (1973b) found that over two breeding seasons invertebrates constituted 80 percent of the total prey by number, but only 5 percent of the biomass. Marti (1974) found that over three seasons in Colorado invertebrates made up 90 percent of the prey by number, but only 9 percent of the biomass. Earhart and Johnson (1970) and Murray (1976), in theoretical discussions of sexual dimorphism and geographical variation in clutch sizes in North American owls, suggest that Burrowing Owls are primarily insectivorous. Though this conclusion can be drawn from reports on food habits which rank the relative importance of prey only in terms of percent of the total of prey items, it does not appear justified when considering the prey composition in terms of total biomass. For predators such as Burrowing Owls which utilize prey differing greatly in size, biomass estimates should be included to present an accurate picture of diet composition.

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Sixty-six percent of the total prey biomass of Burrowing Owls on the INEL Site was represented by three species, Ord kangaroo rat (*Dipodomys ordii*), montane vole (*Microtus montanus*), and Jerusalem cricket (*Stenopelmatus fuscus*). All of the burrows we studied were probably originally excavated by badgers (*Taxidea taxus*) in pursuit of either kangaroo rats or Great Basin pocket mice (*Perognathus parvus*). Thus all the burrows were in or near established colonies of these species. In addition, seven of the burrows were in areas adjacent to cultivated fields of alfalfa (*Medicago sativa*), which frequently harbor large populations of montane voles. Jerusalem crickets, which composed almost half of the prey by number, are extremely common insects in arid regions of western North America. They are large, slow, and conspicuous, traits which make them very vulnerable to predation by Burrowing Owls.

From this study it would appear that Burrowing Owls in southeastern Idaho are primarily nocturnal predators. All of the mammal and the majority of invertebrate prey of the owls are most active at night. The most frequently occurring prey species, Jerusalem crickets, are strictly nocturnal. Grasshoppers and passerine birds, both principally diurnal, contributed little to the total diet, even though both were abundant in the area.

TABLE 1. Food habits of Burrowing Owls in southeastern Idaho as determined by pellet analysis.

| | Number | Percent | Biomass (g) | Percent biomass |
|---|---|---|---|---|
| Mammals | (200) | (8) | (6882) | (68) |
| *Dipodomys ordii* | 44 | 2 | 2420 | 24 |
| *Microtus montanus* | 54 | 2 | 2052 | 20 |
| *Perognathus parvus* | 60 | 3 | 900 | 9 |
| *Peromyscus maniculatus* | 35 | 1 | 595 | 6 |
| *Thomomys talpoides* | 6 | tr | 900 | 9 |
| *Mus musculus* | 1 | tr | 15 | tr |
| Birds | (10) | (tr) | (140) | (1) |
| *Eremophila alpestris* | 6 | tr | 84 | 1 |
| Unidentified passerine | 4 | tr | 56 | tr |
| Amphibians | | | | |
| *Scaphiopus intermontanus* | 19 | tr | 266 | 3 |
| Arachnids | (283) | (12) | (338) | (4) |
| Scorpionidae | 123 | 5 | 178 | 2 |
| Solpugidae | 160 | 7 | 160 | 2 |
| Insects | (1924) | (79) | (2501) | (25) |
| Gryllacrididae | 1122 | 46 | 2244 | 22 |
| Acrididae | 8 | tr | 5 | tr |
| Cicadidae | 29 | 1 | 29 | tr |
| Carabidae | 62 | 3 | 14 | tr |
| Silphidae | 133 | 5 | 40 | tr |
| Scarabaeidae | 129 | 5 | 39 | tr |
| Tenebrionidae | 42 | 2 | 23 | tr |
| Formicidae | 61 | 3 | 6 | tr |
| Unidentified Coleoptera | 338 | 14 | 101 | 1 |
| Totals | 2436 | | 10,127 | |

We thank D. R. Johnson, University of Idaho, for reviewing the manuscript, and W. F. Barr, University of Idaho, for his very generous contribution of time and expertise in identifying innumerable insect fragments. This research was funded by the Division of Biomedics and Environmental Research (DOE) and is a contribution of the INEL Site Ecology Studies Program.

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# FLORA OF THE LEE CREEK VALLEY, ALBERTA

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Abstract.— The floristic composition of the Lee Creek valley in southwestern Alberta, Canada, is presented. The valley flora consists of 299 species of vascular plants representing 173 genera and 46 families. The flora is dominated by forbs (73 percent), followed by grasses (24 percent), shrubs (12 percent), and trees (11 percent). The valley of Lee Creek is divided into upper and lower sections on the basis of elevational, climatic, and biotic differences. Floristic richness of the Lee Creek valley is quite evenly divided between the upper and lower valleys: 105 species limited to the upper valley, 95 to the lower valley, and 99 species shared by both upper and lower valleys.

In this paper the results of my field and herbarium work over the years 1957–1978 are presented for that part of the Lee Creek valley lying inside the southwestern corner of the Province of Alberta. The ecological aspects of the river bottom forest biome along the prairie section of Lee Creek have been reported (Shaw 1976), with a combined plant species list for the river bottom forest on St. Mary River, Lee Creek, and Belly River. This paper borrows the river bottom forest species list for lower Lee Creek and adds to it the greater species lists for the other Lee Creek valley biomes.

## Geology and Geography

Lee Creek originates on the north and east slopes of Old Chief Mountain in Glacier National Park, Montana. It flows from alpine meadows at 2,000–3,000 m in three branches that join where the creek crosses the International Boundary at Alberta's Range 27. The creek then flows through the lower montane forest and aspen parkland biomes of the upper valley to Section 11 Township 2 Range 27 West of 4, where it crosses the treeless stretches of the fescue prairie biome at elevations of 1,400 m down to 900 m. Along the lower stream course the poplar-dominated river bottom forest biome becomes a unique ecological entity on Lee Creek. This biome's presence identifies the lower valley and is continuous downstream, through the town of Cardston, to the creek's confluence with St. Mary River at Section 23 Township 3 Range 25 West of 4. Lee Creek drains about 290 square kilometers of northwest Montana and southwest Alberta.

Streamside and valley floor vegetation patterns are modified by Lee Creek streamflow (Shaw 1976). Monthly water flow varies widely throughout the year (Table 1). From late July through autumn and winter the flow is fairly constant and moderate, but during March warmer weather causes snow melt in the foothills and on the lower mountain slopes to increase stream flow. The most rapid melting of deep mountain snow occurs in late May and early June. This coincides with the season of highest precipitation (Table 2), swelling stream flow to its maximum, which is four to five times the winter flow rate. Severe flooding, with considerable streamside vegetation and habitat alteration, occurred in 1902, 1908, 1950, 1964, and 1975.

The mountain section of the Lee Creek valley, in Montana, is carved through geological formations of the Lewis Range's Belt Series and transported eastward as the Lewis Overthrust and overlying the younger Cretaceous shales and sandstones of the plains (Wyatt 1939). The prairie section of Lee Creek flows through and over a variety of consolidated and unconsolidated deposits, from the transported Belt series rocks of Proterozoic time to the more recent Cretaceous and Tertiary series. Bedrock cut through and exposed along the Alberta section of Lee Creek is mainly an exposure of the highly calcareous light gray sandstones and sandy shales of the St. Mary River nonmarine sandstone, the uppermost of the Cretaceous formations of southwest Alberta. Irregular bedding and cross-bedding are common, and freshwater oyster shells and coal beds are frequently exposed. Much of this bedrock is veneered with glacial deposits left when the Ice Age glaciers melted. There is also widespread distribution of reworked glacial deposits as well as alluvial and lacustrine deposits transported by the creek.

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The soils along the creek valley bottom are of alluvial deposition and some, still liable to frequent flooding, are quite variable in fertility, texture, and utilization.

In southwest Alberta the break from mountains to plains is fairly rapid, there being no wide range of foothills.

## CLIMATE

Summer along Lee Creek is normally warm, but winter is usually long and cold (Table 3). Mean temperatures are below 0 degrees C from November through March at Cardston on lower Lee Creek. A wide variation in winter temperatures occurs, depending on the southerly flow of cold Arctic air and the easterly flow of temperature-moderating Chinook winds. Temperatures rise rapidly from winter to summer and decline with equal rapidity from summer to winter. Monthly mean temperatures at Cardston are above 10 degrees C for the five months from May to September. The average frost-free period on Lee Creek to which the native plants have adapted ranges from 70 days in montane forest on upper Lee Creek to 100 days at Cardston near the creek's confluence. Precipitation along the valley shows wide variation from year to year. Winter snowfall in the lower valley is comparatively light, with amounts ranging from 76 to 127 cm. This increases in the upper valley to 180 cm. Total precipitation at Cardston in the lower valley averages 45.8 cm and gradually increases through the upper valley (Canada Transport 1967). A combination of snowfall and wind causes drift buildup in the stream valley throughout winter.

## ECOLOGY AND TAXONOMY

The Lee Creek valley in Alberta is a postglacial, meandering, stream-carved valley. The stream itself works back and forth from

TABLE 1. Mean monthly stream flow in cubic meters per second of Lee Creek in southwest Alberta, Canada.

| Month | Lee Creek Cardston |
|---|---|
| January | 0.4 |
| February | 0.4 |
| March | 1.1 |
| April | 2.4 |
| May | 4.6 |
| June | 4.5 |
| July | 1.5 |
| August | 0.5 |
| September | 0.5 |
| October | 0.6 |
| November | 0.5 |
| December | 0.3 |

TABLE 2. Mean monthly precipitation in inches and centimeters for Cardston, Alberta, elevation 1,151 m.

| Month | Inches | Centimeters |
|---|---|---|
| January | 0.75 | 1.9 |
| February | 0.91 | 2.3 |
| March | 1.14 | 2.9 |
| April | 1.39 | 3.5 |
| May | 2.38 | 6.1 |
| June | 3.59 | 9.1 |
| July | 1.62 | 4.1 |
| August | 1.50 | 3.8 |
| September | 1.75 | 4.4 |
| October | 1.19 | 3.0 |
| November | 0.94 | 2.4 |
| December | 0.88 | 2.2 |
| Total | 18.04 | 45.8 |

TABLE 3. Mean daily temperature in degrees Centigrade and degrees Fahrenheit at Cardston, Alberta.

| Month | Centigrade | Fahrenheit |
|---|---|---|
| January | -7.4 | 18.7 |
| February | -6.5 | 20.3 |
| March | -2.5 | 27.5 |
| April | 4.5 | 40.2 |
| May | 10.3 | 50.6 |
| June | 13.7 | 56.5 |
| July | 17.9 | 64.1 |
| August | 16.1 | 61.1 |
| September | 11.6 | 52.7 |
| October | 6.6 | 43.8 |
| November | -0.4 | 31.3 |
| December | -4.2 | 24.4 |
| Year | 5.0 | 40.9 |

year to year resorting its gravel base, eroding on the outside bends and depositing on the inside ones as it cuts a deeper channel. Major alteration occurs during the season of high water in late May and early June.

The life span of a gravel bar, the first terrace of the valley floor, is entirely fortuitous, depending on the vagaries of Alberta weather and its effect on streamflow. If the first terrace escapes erosional destruction for 20 years or more, natural succession will change the herb-dominated first terrace plant community to the poplar-dominated lower valley, and poplar and spruce-dominated upper valley, communities on the terrace. As erosion and channel shifting are directed away from the terrace and the stream cuts deeper into the valley floor, what was once a first terrace becomes a second terrace, and it is here the river bottom forest thrives. Years or centuries later the second terrace may be left even higher as a third terrace, and when this happens the river bottom forest fails to be self-sustaining. As the mature trees die out without seed or vegetative replacement, the grassland biome (fescue prairie) in the lower valley, or in the upper valley the deciduous forest biome (aspen parkland), take over with virtual similarity to the vegetation on valley slopes and surrounding terrain.

With the constant erosion, deposition, and channel shifting, fresh bars of material sorted into various textures and of varying depths annually become available for colonization by plants. In spite of this constancy of change, the creek bottom floodplain is a very uniform habitat where climate and substrate determine the establishment of plant species.

The combined upper and lower Lee Creek vascular flora consists of 49 species of woody plants and 250 species of herbaceous ones, for a total of 299 species.

In ecological distribution 105 species were confined to the upper Lee Creek valley, 95 species to the lower Lee Creek valley, and 99 species were found in both the upper and lower valleys.

Naturalized exotics made up 7.7 percent (23 species) and native species 92.3 percent (276 species) of the total species number.

Taxonomically the 299 species were contributed by 46 families and 173 genera. Nine families dominated the flora. A dominant family arbitrarily was one with 10 or more species in the valley (Table 4). Floristic richness is enhanced by the high yearly frequency of new gravel bar pioneer sites and the availability of plant reproductive material from five major biomes: alpine tundra, montane forest, aspen parkland, fescue prairie, and river bottom forest.

Within the Lee Creek valley flora there are 11 plant species listed by Argus and White (1978) as being rare in Alberta. These 11 are *Angelica dawsonii, Balsamorhiza sagittata, Calochortus apiculatus, Disporum oreganum, Hydrophyllum capitatum, Larix occidentalis, Lesquerella alpina, Phlox alyssifolia, Plantago canescens, Populus angustifolia*, and *Senecio hydrophiloides*.

Lee Creek, like many other stream systems, provides excellent seed dispersal habitat. Flowing water can bring mountain or submontane species to greater range extensions down the valley. Windborne seeds are readily dropped in the lee of sheltering banks and thickets as wind velocity decreases. Bird activities provide other transport mechanisms. Downstream species are able to extend their ranges upstream nearly as readily (Table 5).

All parts of the Lee Creek valley in Alberta are grazed by domestic livestock, principally cattle. The upper valley represents mainly summer-use pasture and the lower valley receives year-round grazing use. Deer, both white-tail and mule, are common throughout the length of the valley.

Intensive plant collecting was done at many valley sites throughout the growing

TABLE 4. Dominant plant families of the Lee Creek valley.

| Family | Number of species | Percent of total species |
|---|---|---|
| Compositae | 52 | 17.4 |
| Leguminosae | 32 | 10.7 |
| Gramineae | 24 | 8.0 |
| Liliaceae | 17 | 5.7 |
| Rosaceae | 17 | 5.7 |
| Salicaceae | 15 | 5.0 |
| Ranunculaceae | 13 | 4.3 |
| Scrophulariaceae | 12 | 4.0 |
| Orchidaceae | 10 | 3.3 |
| Total | 192 | 64.2 |

seasons of several years. The valley flowering season usually began in early May and ended by late September. Specimens were preserved according to standard herbarium practice. Almost all identifications were checked against known herbarium reference material. Taxonomy of the poplars follows Brayshaw (1965), the genus *Cryptantha* after Higgins (1971), and the remainder after Moss (1959), Boivin (1969), Booth (1950), and Booth and Wright (1966). The willows were identified by George Argus of the National Museum of Natural Sciences.

Only those flowering plants native to Lee Creek valley, or naturalized and viable exotics, are included in the species list. Cultivated agricultural and ornamental species were deleted.

The valley is considered to be all the area below the rim elevation of the adjoining land surface.

All specimens collected are in the author's personal herbarium at Cardston, Alberta. A nearly complete duplicate set is on deposit in the Brigham Young University Herbarium (BRY) at Provo, Utah.

For convenience, plant families, genera, and species are listed in alphabetical order. Because of the ecological differences along Lee Creek between the upper and lower valleys, plant species listed will be designated as found in the upper valley only (U), lower valley only (L), or in both upper and lower valleys (UL).

## SPECIES LIST

BERBERIDACEAE
- *Berberis repens* Lindl. U

BETULACEAE
- *Betula glandulosa* Michx. U
- *Betula occidentalis* Hook. UL
- *Betula pumila* L. var. *glandulifera* Regel U

BORAGINACEAE
- *Hackelia floribunda* (Lehm.) I.M. Johnston UL
- *Lappula echinata* Gilib. L
- *Lithospermum incisum* Lehm. L
- *Lithospermum ruderale* Lehm. UL

CAMPANULACEAE
- *Campanula rotundifolia* L. UL

CAPPARIDACEAE
- *Cleome serrulata* Pursh L

CAPRIFOLIACEAE
- *Linnaea borealis* L. var. *americana* (Forbes) Rehd. U
- *Lonicera dioica* L. var. *glaucescens* (Rydb.) Butters UL
- *Lonicera involucrata* (Richards.) Banks U
- *Lonicera tartarica* L. L
- *Symphoricarpos occidentalis* Hook. UL
- *Viburnum edule* (Michx.) Raf. U

CARYOPHYLLACEAE
- *Arenaria lateriflora* L. UL
- *Arenaria rubella* (Wahlenb.) J.E. Sm. U
- *Cerastium arvense* L. UL
- *Silene menziesii* Hook. U
- *Stellaria longipes* Goldie U

COMPOSITAE
- *Achillea millefolium* L. UL
- Agoseris glauca (Pursh) Raf. UL
- *Anaphalis margaritacea* (L.) Benth. & Hook. U
- *Antennaria neglecta* Greene U
- *Antennaria pulcherrima* (Hook.) Greene U
- *Antennaria racemosa* Hook. U
- *Antennaria rosea* Greene UL
- *Arnica chamissonis* Less. ssp. *foliosa* (Nutt.) Mag. U
- *Arnica cordifolia* Hook. U

TABLE 5. Dispersal of species up and down the Lee Creek valley beyond their usual geographic ranges.

| Downstream range extensions | Upstream range extensions |
|---|---|
| *Actaea rubra* | *Astragalus flexuosus* |
| *Arctostaphylos uva-ursi* | *Elaeagnus commutata* |
| *Astragalus bourgovii* | *Oxytropis campestris gracilis* |
| *Corallorhiza striata* | *Oxytropis sericea spicata* |
| *Epilobium angustifolium* | *Oxytropis viscida* |
| *Epilobium latifolium* | *Populus angustifolia* |
| *Heracleum lanatum* | *Salix interior* |
| *Larix occidentalis* | |
| *Picea glauca* | |
| *Pinus flexilis* | |
| *Populus balsamifera trichocarpa* | |
| *Populus tremuloides* | |
| *Pseudotsuga menziesii* | |
| *Pyrola asarifolia purpurea* | |
| *Smilacina racemosa amplexicaulis* | |
| *Veratrum eschscholtzii* | |

*Arnica lonchophylla* Greene U
*Arnica sororia* Greene UL
*Artemisia biennis* Willd. L
*Artemisia campestris* L. L
*Artemisia ludoviciana* Nutt. L
*Aster foliaceus* Lindl. U
*Aster laevis* L. var. *geyeri* A. Gray UL
*Aster occidentalis* (Nutt.) T. & G. UL
*Aster pansus* (Blake) Cronq. UL
*Aster sibiricus* L. U
*Balsamorhiza sagittata* (Pursh) Nutt. UL
*Chrysanthemum leucanthemum* L. UL
*Chrysopsis villosa* (Pursh) Nutt. var. *hispida* (Hook.) Gray L
*Cichorium intybus* L. L
*Cirsium arvense* (L.) Scop. UL
*Cirsium undulatum* (Nutt.) Spreng. L
*Crepis elegans* Hook. U
*Erigeron caespitosus* Nutt. L
*Erigeron glabellus* Nutt. var. *pubescens* (Hook.) Cronq. U
*Erigeron peregrinus* (Pursh) Greene ssp. *callianthemus* (Greene) Cronq. L
*Erigeron philadelphicus* L. U
*Erigeron speciosus* (Lindl.) DC. L
*Erigeron strigosus* Muhl. L
*Erigeron subtrinervis* Rydb. var. *conspicuus* (Rydb.) Cronq. U
*Gaillardia aristata* Pursh UL
*Helianthus laetiflorus* Pers. var. *subrhomboideus* (Rydb.) Fern. L
*Hieracium scouleri* AA. U
*Hieracium umbellatum* L. L
*Hymenoxys acaulis* (Pursh) Parker L
*Liatris punctata* Hook. L
*Ratibida columnifera* (Nutt.) Wooton & Standl. L
*Rudbeckia serotina* Nutt. U
*Senecio canus* Hook. UL
*Senecio hydrophiloides* Rydb. U
*Senecio integerrimus* Nutt. var. *exaltatus* (Nutt.) Cronq. L
*Senecio lugens* Richards. UL
*Senecio pauperculus* Michx. U
*Senecio triangularis* Hook. U
*Solidago decumbens* Greene var. *oreophila* (Rydb.) Fern. L
*Solidago missouriensis* Nutt. UL
*Solidago multiradiata* Ait. U
*Taraxacum officinale* Weber UL
*Tragopogon dubius* Scop. L

Cornaceae
*Cornus canadensis* L. U
*Cornus stolonifera* Michx. UL

Crassulaceae
*Sedum stenopetalum* Pursh U

Cruciferae
*Arabis divaricata* A. Nels. U
*Arabis hirsuta* (L.) Scop. var. *glabrata* T. & G. UL
*Arabis holboellii* Hornem. var. *retrofracta* (Graham) Rydb. L
*Erysimum cheiranthoides* L. U
*Erysimum inconspicuum* (S. Wats.) MacM. U
*Lesquerella alpina* (Nutt.) S. Wats. var. *spathulata* (Rydb.) Payson L
*Physaria didymocarpa* (Hook.) A. Gray U
*Rorippa nasturtium-aquaticum* (L.) Schinz & Thell. L

Cyperaceae
*Carex filifolia* Nutt. UL
*Carex hystricina* Muhl. U
*Carex rostrata* Stokes L
*Scirpus microcarpus* Presl L
*Scirpus validus* Vahl U

Elaeagnaceae
*Elaeagnus commutata* Bernh. UL
*Shepherdia argentea* Nutt. L
*Shepherdia canadensis* (L.) Nutt. U

Equisetaceae
*Equisetum arvense* L. UL
*Equisetum fluviatile* L. U

Ericaceae
*Arctostaphylos uva-ursi* (L.) Spreng. UL

Euphorbiaceae
*Euphorbia esula* L. L

Gentianaceae
*Gentiana detonsa* Rottb. L
*Gentianella amarella* (L.) Borner ssp. *acuta* (Michx.) J. M. Gillett U

Geraniaceae
*Geranium nervosum* Rydb. U
*Geranium richardsonii* Fisch. & Trautv. U
*Geranium viscosissimum* Fisch. & Mey. U

Gramineae
*Agropyron smithii* Rydb. L
*Agropyron subsecundum* (Link.) Hitchc. L
*Agrostis alba* L. L
*Beckmannia syzigachne* (Steud.) Fern. L
*Bouteloua gracilis* (HBK). Lag. L
*Bromus commutatus* Schrad. L
*Bromus inermis* Leyss. L
*Calamagrostis purpurascens* R. Br. U
*Danthonia parryi* Scribn. U
*Danthonia spicata* (L.) Beauv. U
*Deschampsia caespitosa* (L.) Beauv. U
*Festuca idahoensis* Elmer L
*Festuca ovina* L. L
*Festuca scabrella* Torr. UL
*Glyceria grandis* S. Wats. UL
*Helictotrichon hookeri* (Scribn.) Henr. U
*Koeleria cristata* (L.) Pers. L
*Oryzopsis hymenoides* (R. & S.) Ricker L
*Phleum pratense* L. UL
*Poa arctica* R. Br. U
*Poa compressa* L. U
*Poa pratensis* L. UL
*Stipa columbiana* Macoun U
*Stipa richardsonii* Link U

Hydrophyllaceae
*Hydrophyllum capitatum* Dougl. U
*Phacelia sericea* (Graham) A. Gray U

Iridaceae
*Sisyrinchium montanum* Greene U

Juncaceae
*Juncus alpinus* Vill. var. *rariflorus* Hartm. L
*Juncus longistylis* Torr. L

Labiatae
*Mentha arvensis* L. var. *villosa* (Benth.) S.R. Stewart UL
*Monarda fistulosa* L. var. *menthaefolia* (Graham) Fern. UL

*Prunella vulgaris* L. UL
LEGUMINOSAE
*Astragalus aboriginum* Richards. UL
*Astragalus alpinus* L. U
*Astragalus bisulcatus* (Hook.) A. Gray L
*Astragalus bourgovii* A. Gray UL
*Astragalus canadensis* L. L
*Astragalus crassicarpus* Nutt. L
*Astragalus drummondii* Dougl. L
*Astragalus flexuosus* Dougl. UL
*Astragalus missouriensis* Nutt. L
*Astragalus robinsii* (Oakes) Gray UL
*Astragalus striatus* Nutt. L
*Astragalus triphyllus* Pursh L
*Astragalus vexilliflexus* Sheld. U
*Glycyrrhiza lepidota* (Nutt.) Pursh L
*Hedysarum alpinum* L. UL
*Hedysarum sulphurescens* Rydb. U
*Lathyrus ochroleucus* Hook. UL
*Lupinus argenteus* Pursh L
*Lupinus sericeus* Pursh U
*Medicago lupulina* L. L
*Medicago sativa* L. L
*Melilotus alba* Desr. L
*Melilotus officinalis* (L.) Lam. L
*Oxytropis campestris* (L.) DC. var. *gracilis* (A. Nels.) Barneby UL
*Oxytropis sericea* Nutt. var. *spicata* (Hook.) Barneby UL
*Oxytropis splendens* Dougl. UL
*Oxytropis viscida* Nutt. UL
*Petalostemon purpureum* (Vent.) Rydb. L
*Thermopsis rhombifolia* (Nutt.) Richards. UL
*Trifolium hybridum* L. L
*Trifolium pratense* L. L
*Vicia americana* Muhl. UL
LILIACEAE
*Allium cernuum* Roth UL
*Allium schoenoprasum* L. var. *sibiricum* (L.) Hartm. U
*Allium textile* Nels. & Macbr. L
*Calochortus apiculatus* Baker U
*Camassia quamash* (Pursh) Greene U
*Clintonia uniflora* (Schult.) Kunth U
*Disporum oreganum* (S. Wats.) B. & H. L
*Erythronium grandiflorum* Pursh U
*Fritillaria pudica* (Pursh) Spreng. UL
*Lilium philadelphicum* L. var. *andinum* (Nutt.) Ker U
*Smilacina racemosa* (L.) Desf. var. *amplexicaulis* (Nutt.) S. Wats. UL
*Smilacina stellata* (L.) Desf. UL
*Stenanthium occidentale* A. Gray U
*Streptopus amplexifolius* (L.) DC. U
*Veratrum eschscholtzii* A. Gray U
*Zygadenus elegans* Pursh UL
*Zygadenus gramineus* Rydb. L
LINACEAE
*Linum lewisii* Pursh UL
MALVACEAE
*Sphaeralcea coccinea* (Pursh) Rydb. L
ONAGRACEAE
*Epilobium angustifolium* L. U
*Epilobium glandulosum* Lehm. L
*Epilobium latifolium* L. UL
*Gaura coccinea* Pursh var. *glabra* (Lehm.) Torr. & Gray L
*Oenothera biennis* L. L
*Oenothera caespitosa* Nutt. L
ORCHIDACEAE
*Calypso bulbosa* (L.) Oakes U
*Corallorhiza maculata* Raf. U
*Corallorhiza striata* Lindl. UL
*Corallorhiza trifida* Chatelain U
*Cypripedium passerinum* Richards. U
*Habenaria dilatata* (Pursh) Hook. U
*Habenaria obtusata* (Pursh) Richards. U
*Habenaria unalascensis* (Spreng.) S. Wats. U
*Habenaria viridis* (L.) R. Br. var. *bracteata* (Muhl.) A. Gray UL
*Orchis rotundifolia* Banks U
PINACEAE
*Juniperus communis* L. var. *depressa* Pursh UL
*Juniperus horizontalis* Moench UL
*Larix occidentalis* Nutt. U
*Picea glauca* (Moench) Voss UL
*Pinus contorta* Loudon var. *latifolia* Engelm. U
*Pinus flexilis* James UL
*Pseudotsuga menziesii* (Mirb.) Franco UL
PLANTAGINACEAE
*Plantago major* L. UL
*Plantago septata* Morris L = *P. canescens* Adams
POLEMONIACEAE
*Collomia linearis* Nutt. U
*Phlox alyssifolia* Greene UL
*Phlox hoodii* Richards. UL
*Polemonium pulcherrimum* Hook. L
POLYGONACEAE
*Eriogonum flavum* Nutt. L
*Polygonum bistortoides* Pursh U
*Rumex crispus* L. L
PRIMULACEAE
*Dodecatheon conjugens* Greene UL
*Dodecatheon radicatum* Greene U
*Lysimachia ciliata* L. UL
PYROLACEAE
*Moneses uniflora* (L.) A. Gray U
*Pyrola asarifolia* Michx. var. *purpurea* (Bunge) Fern. UL
*Pyrola virens* Schweigg. U
RANUNCULACEAE
*Actaea rubra* (Ait.) Willd. UL
*Anemone multifida* Poir. UL
*Anemone parviflora* Michx. U
*Anemone patens* L. var. *wolfgangiana* (Bess.) Koch UL
*Aquilegia flavescens* S. Wats. UL
*Clematis ligusticifolia* Nutt. L
*Clematis verticellaris* DC. var. *columbiana* (Nutt.) A. Gray UL
*Delphinium bicolor* Nutt. UL
*Ranunculus acris* L. UL
*Ranunculus flammula* L. var. *filiformis* (Michx.) Hook. UL
*Ranunculus pedatifidus* J.E. Smith var. *affinis* (R. Br.) L. Benson U
*Ranunculus sceleratus* L. var. *multifidus* Nutt. L
*Thalictrum venulosum* Trel. U
RHAMNACEAE
*Rhamnus cathartica* L. L

ROSACEAE
*Amelanchier alnifolia* Nutt. UL
*Crataegus chrysocarpa* Ashe L
*Dryas drummondii* Richards. UL
*Fragaria virginiana* Duchesne var. *glauca* S. Wats. UL
*Geum allepicum* Jacq. UL
*Geum rivale* L. U
*Geum triflorum* Pursh UL
*Potentilla concinna* Richards. L
*Potentilla fruticosa* L. UL
*Potentilla glandulosa* Lindl. ssp. *pseudorupestris* (Rydb.) Keck U
*Potentilla gracilis* Dougl. var. *flabelliformis* (Lehm.) Nutt. U
*Potentilla gracilis* Dougl. var. *pulcherrima* (Lehm.) Fern. U
*Prunus virginiana* L. var. *melanocarpa* (A. Nels.) Sarg. UL
*Rosa acicularis* Lindl. UL
*Rosa woodsii* Lindl. UL
*Rubus parviflorus* Nutt. U
*Rubus strigosus* Michx. UL
RUBIACEAE
*Galium boreale* L. UL
*Galium triflorum* Michx. L
SALICACEAE
*Populus acuminata* Rydb. L
*Populus angustifolia* James L
*Populus angustifolia* James X *balsamifera* L. L
*Populus balsamifera* L. subsp. *balsamifera* L
*Populus balsamifera* L. subsp. *trichocarpa* (T.&G. ex Hook.) Brayshaw UL
*Populus tremuloides* Michx. UL
*Salix barclayi* Anderss. U
*Salix bebbiana* Sarg. L
*Salix discolor* Muhl. L
*Salix glauca* Anderss. U
*Salix interior* Rowlee L
*Salix lasiandra* Benth. L
*Salix lutea* Nutt. L
*Salix melanopsis* Nutt. L
*Salix pseudomonticola* Ball L
SANTALACEAE
*Comandra pallida* A. DC. UL
SAXIFRAGACEAE
*Parnassia palustris* L. var. *neogaea* Fern. L
*Ribes lacustre* (Pers.) Poir. U
SCROPHULARIACEAE
*Besseya wyomingensis* (A. Nels.) Rydb. L
*Castilleja miniata* Dougl. UL
*Castilleja septentrionalis* Lindl. U
*Orthocarpus luteus* Nutt. L
*Pedicularis bracteosa* Benth. U
*Pedicularis groenlandica* Retz. U
*Penstemon confertus* Dougl. UL
*Penstemon nitidus* Dougl. UL
*Rhinanthus crista-galli* L. U
*Verbascum thapsus* L. L
*Verbena bracteata* Lag. & Rodr. U
*Veronica americana* (Raf.) Schw. UL
UMBELLIFERAE
*Angelica dawsonii* S. Wats. U
*Cicuta douglasii* (DC.) Coult. & Rose UL
*Heracleum lanatum* Michx. UL
*Lomatium simplex* (Nutt.) Macbr. var. *leptophyllum* (Hook.) Mathias L
*Lomatium triternatum* (Pursh) Coult. & Rose U
*Osmorhiza depauperata* Phillippi U
*Perideridia gairdneri* (Hook. & Arn.) Mathias UL
*Zizia aptera* (A. Gray) Fern. UL
VALERIANACEAE
*Valeriana septentrionalis* Rydb. U
VIOLACEAE
*Viola adunca* J.E. Smith UL
*Viola nephrophylla* Greene U
*Viola orbiculata* Geyer L
*Viola rugulosa* Greene UL
*Viola selkirkii* Pursh U

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# CLIMATES OF FESCUE GRASSLANDS OF MOUNTAINS IN THE WESTERN UNITED STATES

T. Weaver[1]

Abstract.— Climates of fescue grasslands were described by summarizing USDC Weather Bureau records of representative sites. Mean temperatures of the warmest month declined from 18 to 14 C, average annual precipitation increased from 40–50 to 170 cm, and the number of arid months in an arbitrarily defined dry year declined from 3 to 1–2 as one moves from *Festuca arizonica* (14 stations) to *F. scabrella* (15) to *F. idahoensis* (17) to *F. thurberi* (6) to *F. viridula* (9). Climates of the grasslands are sufficiently like those of the *Pseudotsuga menziesii* and *Abies lasiocarpa* zones of the northern Rocky Mountains to make one ask what factors—wind, snow duration, soil characteristics, or fire—allow the fescue grasslands to persist in a conifer climatic zone.

Fescue grasslands form an important part of mountain vegetation in the western United States. The geographical and altitudinal ranges of major species are shown by Hitchcock (1950) and Kuchler (1964) among others. *Festuca arizonica* Vasey occurs in the southern Rocky Mountains under pine forests or in meadows in Kuchler's types 18 and 19. *Festuca thurberi* Vasey is found in higher forests to timberline in the southern and central Rocky Mountains. *Festuca scabrella* Torr. and *Festuca idahoensis* Elmer occur in the northern Rocky Mountains in Kuchler's foothill grassland (63) type as well as in meadows in the forest zone. *Festuca viridula* Vasey is generally found west of the Rocky Mountains in alpine and subalpine meadows, above the ranges of *Festuca scabrella* and *Festuca idahoensis*.

The objects of this paper are (1) to summarize data available for USDC Weather Bureau stations (6 to 17) in each grassland type and (2) to compare the climates of the fescue grasslands. Climates of adjacent vegetation types have been summarized by similar methods (Weaver 1979). Other studies of the climates of fescue grasslands include a 3-year study of summer climates of two *Festuca scabrella* grasslands in British Columbia (van-Ryswyk et al. 1966), a 5 (now 10-)-year study of growing season climates of four *Festuca idahoensis* grasslands in southwest Montana (Mueggler 1971), and a 23-year study of climate effects in a *Festuca idahoensis* stand in south Idaho (Blaisdell 1958).

## Methods

Maps of weather station locations were sent to U.S. Forest Service and University personnel familiar with fescue grasslands, along with letters asking each to identify weather stations which lay in that person's fescue type. I gratefully acknowledge the help of E. Aldon, W. Clary, and W. Moir with *F. arizonica* stations; of P. Currie, W. Moir, H. Paulsen, and G. Turner with *F. thurberi* stations; of M. Morris with *F. scabrella* stations; of M. Morris, W. Mueggler, and G. Payne with *F. idahoensis* stations; and J. Strickler with *F. viridula* stations. A few of the sites studied were not visited by those recommending them, but the availability of herbarium material from the sites and the small between-site standard errors (less than the between-year standard errors for a station in the type) suggest that there were few or no misclassifications.

The 1961–1970 climatological data (USDC 1961–1970) for each station were summarized by calculating the mean and standard errors for monthly precipitation, average monthly maximum temperature, average monthly minimum temperature, and monthly frost days. These were returned to the cooperators for comment. A relatively short period of record was used (1) because it seemed wise to compare all stations for the same period, (2) because many stations lacked a longer record, and (3) because without containment the number of data points involved would have become unmanageable; 490 data points were collected for each of the 61 stations considered in this study.

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A grand summary of the climatological data was made by calculating average means and average standard errors across the stations in each type. These data, along with those of the driest and wettest station in each type, are summarized in Figure 1. The driest and wettest station in each type were chosen arbitrarily as those with the lowest and highest average annual precipitation.

The weather stations used were: (1) For *Festuca arizonica*, Chevlon RS, Flagstaff, Fort Valley, Grand Canyon, Jacob Lake, and McNary, Arizona; Pagosa Springs and Red Feather Lakes, Colorado; and Gascon, Lake Maloya, Los Alamos, Luna RS, Ruidoso, and Wolf Canyon, New Mexico. (2) For *Festuca*

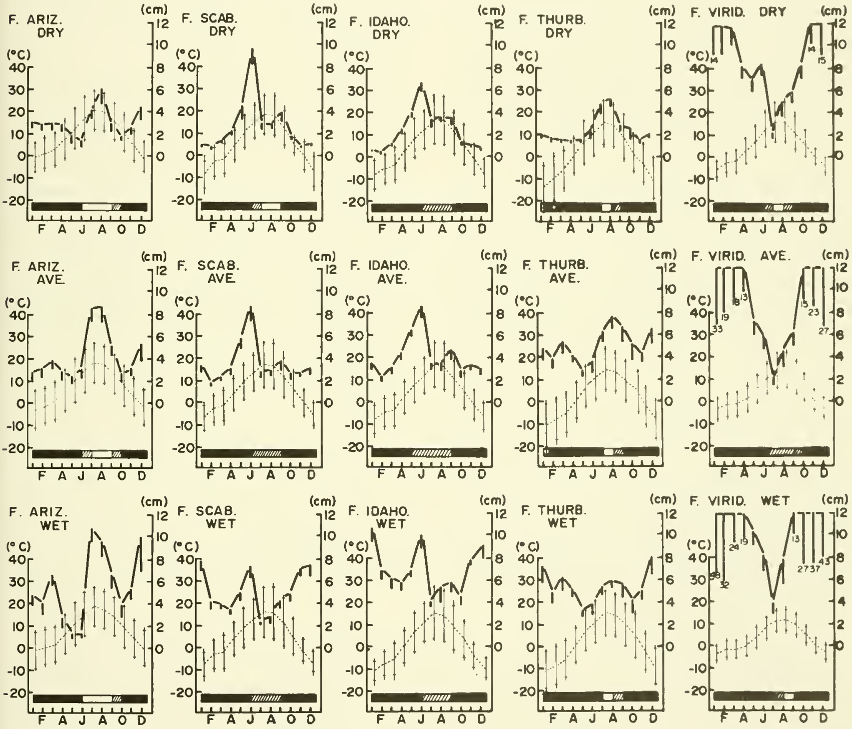

Fig. 1. Climates of fescue grasslands 1961–1970. The dashed line shows the annual course of mean daily temperature; bars reaching above and below it show mean monthly maximum and minimum temperatures; and short bars reaching beyond the cross bars show the mean standard errors of the maximum and minimum. The heavy solid line indicates mean monthly precipitation and heavy bars extending below this line show the standard errors of these means; associated numbers in the *F. viridula* graphs indicate precipitation levels that lie off the graphs. Arid months (Walter, 1973) are those in which the temperature line rises above the precipitation line. The heavy bar across the base of the graph indicates the number of frost (0 C) days: clear months experience less than one frost per month, hatched months experience from one to six frosts, and solid months experience more than six frosts.

*thurberi*, Cochetopa Creek, Crested Butte, Silverton, Taylor Park, Telluride, and Wolf Creek Pass, Colorado. (3) For *Festuca scabrella*, Babb, Browning, Del Bonito, Elliston, Gibson Dam, Gold Butte, Kalispell, Lewiston, Lincoln, Ovando, Phillipsburg, Polebridge, Polson, St. Ignatius, and Sula, Montana. (4) For *Festuca idahoensis*, Bozeman MSU, Gallatin Gateway, Hebgen Dam, Jackson, Lakeview, Lima, Melville, Mystic Lake, Pony, Red Lodge, Virginia City, White Sulphur Springs, and Wisdom, Montana; Buffalo 15SW, Burgess Junction, Lamar RS, Wyoming, and Kilgore, Idaho. Powder River Pass, Soldier Park, and Willow Park, Wyoming (J. Thilenius); Plummer 3WSW, Moscow, Grangeville, Hill City, Fairfield 8S, and Three Creek, Idaho (M. Hironaka); Dayton, Lacrosse, Pomeroy, Walla Walla, Cheney, Moscow, Pullman, Rosalia, and Goldendale, Washington (Daubenmire 1970); and Bangtail Ridge, Montana, could probably have been included but were not. (5) For *Festuca viridula*, Soda Springs, Squaw Valley, Twin Lakes, California; Crater Lake and Santiam Pass, Oregon; Rainier Paradise RS and Stevens Point, Washington; and Burke, Idaho. Summer precipitation data for additional stations, usually maintained by the U.S. Forest Service, are recorded in USDC Climatological Data records.

## Results

It was noted earlier that in the southern Rocky Mountains one finds *F. arizonica* at the lower edge of the forest zone and that in higher forests and meadows one finds *F. thurberi*; in the northern Rocky Mountains, *F. idahoensis* and *F. scabrella* range from foothill grasslands to mountain meadows; west of the Rocky Mountains one may find *F. viridula* in alpine and subalpine meadows above the normal range of either *F. idahoensis* or *F. scabrella*.

The following paragraphs, as well as Table 1 and Figure 1, point out similarities and differences in the climates of the grasslands occupied by these species. The discussion emphasizes an average climate calculated from measurements made at 6 to 17 weather stations. The average climate for a type will tend to underestimate precipitation and frost days and to overestimate temperatures because relatively high and inaccessable sites usually lack weather stations. For this reason, the reader should consider carefully the cli-

Table 1. Mean climatic characteristic of fescue grasslands.

| | *F. arizonica* | *F. scabrella* | *F. idahoensis* | *F. thurberi* | *F. viridula* |
|---|---|---|---|---|---|
| Number of stations | 14 | 15 | 17 | 6 | 9 |
| Mean temp., coolest month (C) | –3 | –6 | –8 | –10 | –3 |
| Daily range (C) | 17 | 11 | 12 | 20 | 9 |
| Months with less than six frosts | 4 | 3 | 4 | 2 | 4 |
| Mean temp. of coolest frostfree month (C) | 13 | 13 | 8 | 12 | 10 |
| Mean temp., warmest month (C) | 18 | 17 | 17 | 14 | 14 |
| Daily range (C) | 17 | 20 | 20 | 19 | 16 |
| Mean SE of maximum temperatures | | | | | |
| Between years | 0.6 | 0.8 | 0.7 | 0.6 | 0.6 |
| Between stations | 0.5 | 0.3 | 0.6 | 1.0 | 0.8 |
| Mean SE of minimum temperatures | | | | | |
| Between years | 0.5 | 0.6 | 0.6 | 0.5 | 0.5 |
| Between stations | 0.7 | 0.5 | 0.6 | 0.7 | 0.4 |
| Number of arid months | | | | | |
| Mean | 0 | 2 | 0 | 0 | 1 |
| Dry year | 3 | 3 | 2 | 1 | 2 |
| Average annual precipitation (cm) | 51 | 43 | 48 | 61 | 170 |
| Mean SE of precipitation (mm) | | | | | |
| Between years | 9 | 7 | 6 | 9 | 25 |
| Between stations | 4 | 3 | 4 | 9 | 15 |

matic ranges demonstrated by data from extreme stands (Fig. 1).

Regardless of vegetation type average winter air temperature in weather shelters at heights of 1 to 2 m are in the –3 to –10 C range. Night temperatures are 5–10 C cooler than this, and day temperatures are 5–10 C warmer. The daily range is proportional to the distance from the Pacific Ocean, i.e., to continentality. Herbaceous plants and small animals in fescue grasslands usually experience winter temperatures varying only slightly around 0 C because a snow layer insulates them from cold air masses.

The "frost-free" season is from two to four months long in a fescue grassland: For *F. thurberi* it is two months, for *F. scabrella* it is three months; and for the remaining fescues it is from three to four months.

Cooler months in the frost-free season have average temperatures of 8–13 C. Warmer months in this period have average temperatures of 17–18 C in the lower *F. arizonica*, *F. scabrella*, and *F. idahoensis* sites and 14 C in the higher *F. thurberi* and *F. viridula* sites. Nightly minimum temperatures average 8–10 cooler and maximum temperatures are 8–10 C warmer than average temperatures.

The average standard errors of daily maximum temperatures taken a month at a time are 0.7 between years and 0.6 between stations. The average standard errors of daily minimum temperatures taken a month at a time are 0.5 between years and 0.6 between stations. The fact that between-year variability exceeds between-station variability is an indication of the homogeneity of temperature data gathered in each vegetation type. Temperatures deviating more than two standard errors from the mean are improbable (3 percent).

In an average year *F. scabrella* experiences two arid months, *F. viridula* experiences one arid month, and the remaining fescues experience no arid months; during these months plant growth is especially dependent on water stored in the soil profile during the preceeding months. This statement depends on the definition of an arid month as one in which the temperature line, on a graph plotted with the scales used, rises above the precipitation line; this device was developed by H. Walter (1973) and similar devices are discussed by Daubenmire (1956). Note that if one uses Walter's index the length of arid periods are the same for the driest, the average, and the wettest stand considered in each type, except for *F. arizonica* (dry) and *F. viridula* (wet).

A "dry year" may be defined as one in which precipitation is always two standard errors below the mean, because the probability of such low precipitation in one month is about 3 percent. Such a year for the average fescue stand in a type would be drier than the dry stand presented for that type, with the exception of the dry *F. arizonica* stand. In such a dry year arid months experienced in the frost-free season would be two for *F. scabrella*, *F. idahoensis*, and *F. viridula*; one for *F. arizonica*; and none for *F. thurberi*. Total arid months experienced would be three for *F. arizonica* and *F. scabrella*, two for *F. idahoensis* and *F. viridula*, and one for *F. thurberi*.

Total precipitation ranges from 43 cm in the *F. scabrella* type to 177 cm in the *F. viridula* type, but total precipitation is a poor indicator of water availability during the growing season. This is shown by two facts: first, the fescue types with the greatest number of arid months (as defined by Walter, 1973) during an average year include the driest type (*F. scabrella*) and the wettest type (*F. viridula*), the latter because it receives much of its precipitation during the winter months. Deep, fine-textured soils may compensate for this type of aridity if winter precipitation brings them to field capacity. And, second, within each type the wettest stand differs from both the dry and the average stand by the relatively great amounts of precipitation it receives during the winter months.

## CONCLUSIONS

A review of climatic data from 61 weather stations representing five fescue grassland types and spanning 25 degrees of latitude leads one to three qualified conclusions. (1) Variation in climate between sites in a fescue grassland type is usually less than variation between years at a site in that type. (2) The climates of fescue grasslands are generally similar, with mean temperatures in the coldest month between –3 and –10 C, mean temperatures in the warmest month between 14 and 18 C, daily temperature ranges of about 18 degrees, two to four months with fewer than six frost days, and months in which evapotranspiration exceeds precipitation usually less than two. (3) Ecologically important differences between the climates of the fescue types lie in summer conditions. Average July temperatures are higher *F. arizonica*, *F. scabrella*, and *F. idahoensis* grasslands (17–18 C) than in *F. thurberi* and *F. viridula* grasslands (14 C). And arid months decline from three in *F. arizonica* and *F. scabrella* to 1 or 2 in *F. idahoensis*, *F. thurberi*, and *F. viridula* grasslands.

A comparison of the fescue climate with that of other vegetation types of the northern Rocky Mountains (Weaver 1979) shows that the fescue grasslands generally appear in a coniferous forest climate: (1) its frost-free season is similar to that of *Pseudotsuga menziesii* and *Abies lasiocarpa* zones, (2) its average July temperatures are similar to those of the *Pseudotsuga* and *Abies* zones, (3) its average annual precipitation is similar to that of the *Pseudotsuga* and *Abies* zones, and (4) its drought periods are similar to those of the *Pseudotsuga* and *Abies* zones. Environmental factors other than temperature and precipitation—perhaps wind, snow cover, soil characteristics, or fire—must allow fescue grasslands to dominate the sites they do.

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# STONEFLY (PLECOPTERA) RECORDS FROM THE BASIN RANGES OF NEVADA AND UTAH

Andrew L. Sheldon[1]

Abstract.— Distributional records are given for 40 stonefly species on 15 isolated mountain ranges in Nevada and Utah.

The isolated ranges within the Great Basin have attracted little attention from aquatic biologists, and the running water fauna of the region is very poorly known. Cather, Stark, and Gaufin (1975) summarized records of Nevada stoneflies, and Baumann, Surdick, and Gaufin (1977) cite a few additional records for Nevada and western Utah. The stonefly faunas of regions surrounding the Great Basin are described by Jewett (1959, 1960), Newell and Minshall (1976), and Stewart, Baumann, and Stark (1974).

In this paper I document stonefly distributions on 14 mountain ranges in Nevada and the Deep Creek Mountains, Utah, based on repeated collecting trips in 1974 and 1977. These and published data are to be used in a numerical analysis of stonefly distribution within the Great Basin. Records are listed by mountain range and but one record is given for each range. Records redundant with those of Cather et al. (1975) are not listed although I visited many of their localities. Nymphal records are included because the region is so little known and because these data are included in the quantitative analysis.

This research was supported by Grant 7717 from the Penrose Fund of the American Philosophical Society. I thank Dr. R. W. Baumann for examining some of the specimens.

## NEMOURIDAE

*Malenka* sp. A.— Nevada: Clark Co., Spring Mtns., Cold Cr., 2♂♂, 3-V-77. This species will be described by R. W. Baumann from these and previously collected specimens from the Spring Mtns. I have *Malenka* nymphs from Deer Cr. and Willow Cr., Spring Mtns.

*Malenka californica* (Claassen).— Nevada: Lander Co., Toiyabe Ra., Birch Cr., ♀, probably this species, 24-VI-77; White Pine Co., Schell Creek Ra., Kalamazoo Cr., ♂, 2 ♀♀, 26-VI-77.

*Podmosta delicatula* (Claassen).— Nevada: Humboldt Co., Santa Rosa Ra., Dutch John Cr., 5 ♀♀, 19-VI-77.

*Prostoia besametsa* (Ricker).— Nevada: Elko Co., Jarbidge Mtns., Canyon Cr., ♀, 11-VI-74; Ruby Mtns., Thomas Cr., ♂, 2 ♀♀, 12-VI-74.

*Zapada cinctipes* (Banks).— Nevada: Elko Co., Ruby Mtns., Lamoille Cr., nymphs, 17-II-77; Esmeralda Co., White Mtns., Chiatovich Cr., 4 ♂♂, ♀, 10-II-77; Humboldt Co., Jackson Mtns., Bottle Cr., nymphs, 5-II-77; Pine Forest Ra., Alder Cr., 4 ♂♂, 2 ♀♀, 5-II-77; Santa Rosa Ra., Canyon Cr., ♀, 4-II-77; Lander Co., Toiyabe Ra., Kingston Cr., ♂, 8-II-77; Nye Co., Quinn Canyon-Grant Ra., Cherry Cr., 9 ♂♂, 3 ♀♀, 12-II-77; Pershing Co., Humboldt Ra., Star Cr., 2 ♀♀, 28-IV-77; Sonoma Ra., Sonoma Canyon Cr., nymphs, 6-II-77; White Pine Co., Schell Creek Ra., McCoy Cr., nymphs, 16-II-77; Snake Ra., Baker Cr., 2 ♂♂, ♀, 4-V-77; White Pine Ra., White R., nymphs, 13-II-77. Utah: Juab Co., Deep Creek Mtns., Trout Cr., 5 ♀♀, 15-II-77.

*Zapada frigida* (Claassen).— Nevada: Elko Co., Jarbidge Mtns., Canyon Cr., ♂, 11-VI-74.

*Zapada haysi* (Ricker).— Nevada: Elko

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Co., Jarbidge Mtns., Bear Cr., ♀, 10-VI-74; Ruby Mtns., Thomas Cr., ♀, 12-VI-74; White Pine Co., Schell Creek Ra., McCoy Cr., ♂, 5-V-77.

*Zapada oregonensis* (Claassen).— NEVADA: Humboldt Co., Pine Forest Ra., Wood Canyon, ♂, 3 ♀ ♀, 20-VI-77.

## TAENIOPTERYGIDAE

*Doddsia occidentalis* (Banks).— NEVADA: Elko Co., Ruby Mtns., Lamoille Cr., ♀, 6-V-77; White Pine Co., Schell Creek Ra., McCoy Cr., 2 ♂ ♂, ♀, 5-V-77; Snake Ra., Baker Cr., ♀, 4-V-77.

*Taenionema nigripenne* (Banks).— NEVADA: Humboldt Co., Jackson Mtns., Bottle Cr., ♀, 27-IV-77; Santa Rosa Ra., Lye Cr., ♂, 6 ♀ ♀, 19-VI-77; Sonoma Ra., Water Canyon, 8 ♂ ♂, 2 ♀ ♀, 28-IV-77; White Pine Co., Snake Ra., Baker Cr., ♂ ♂, ♀ ♀, 13-VI-74.

## CAPNIIDAE

*Capnia* sp. A.— NEVADA: Esmeralda Co., White Mtns., Middle Cr., 3 ♂ ♂, 14 ♀ ♀, 10-II-77. This species will be described by R. W. Baumann and myself.

*Capnia gracilaria* Claassen.— NEVADA: Elko Co., Ruby Mtns., Lamoille Cr., ♂, 17-II-77; Humboldt Co., Jackson Mtns., Bottle Cr., ♂, 5-II-77; Pine Forest Ra., Wood Canyon, ♂, ♀, 5-II-77; Santa Rosa Ra., Canyon Cr., ♂, 4-II-77; White Pine Co., Schell Creek Ra., McCoy Cr., 2 ♂ ♂, 2 ♀ ♀, 5-V-77; Snake Ra., Baker Cr., 10 ♂ ♂, 13 ♀ ♀, 5-V-77. UTAH: Juab Co., Deep Creek Mtns., Trout Cr., 4 ♂ ♂, 12 ♀ ♀, 15-II-77.

*Capnia uintahi* Gaufin.— NEVADA: Elko Co., Ruby Mtns., Lamoille Cr., ♂, 3 ♀ ♀, 17-II-77; Lander Co., Toiyabe Ra., Big Cr., 18 ♂ ♂, 6 ♀ ♀, 7-II-77; White Pine Co., Schell Creek Ra., McCoy Cr., 17 ♂ ♂, 4 ♀ ♀, 16-II-77.

*Capnia utahensis* Gaufin and Jewett.— NEVADA: Esmeralda Co., White Mtns., Chiatovitch Cr., 2 ♂ ♂, 2 ♀ ♀, 10-II-77; Lander Co., Toiyabe Ra., Ophir Cr., 7 ♂ ♂, 17 ♀ ♀, 9-II-77; Nye Co., Quinn Canyon-Grant Ra., Cherry Cr., 10 ♂ ♂, 4 ♀ ♀, 12-II-77; White Pine Co., Schell Creek Ra., McCoy Cr., 5 ♂ ♂, 4 ♀ ♀; Snake Ra., Baker Cr., 4 ♀ ♀, 4-V-77; White Pine Ra., White R., 1 ♂, 2 ♀ ♀, 13-II-77. UTAH: Juab Co., Deep Creek Mtns., Granite Cr., ♂, 2 ♀ ♀, 15-II-77.

*Capnia wanica* Frison.— NEVADA: Nye Co., Toiyabe Ra., Peavine Cr., 2 ♂ ♂, ♀, 9-II-77; Pershing Co., Humboldt Ra., Buena Vista Cr., 10 ♂ ♂, 2 ♀ ♀, 6-II-77.

*Eucapnopsis brevicauda* (Claassen).— NEVADA: Humboldt Co., Santa Rosa Ra., Lye Cr., ♂, 26-IV-77; Pershing Co., Humboldt Ra., Star Cr., ♀, 18-VI-77.

*Utacapnia lemoniana* (Nebeker and Gaufin).— NEVADA: Elko Co., Ruby Mtns., Lamoille Cr., 3 ♂ ♂, 17-II-77; Lander Co., Toiyabe Ra., Birch Cr., 3 ♂ ♂, ♀, 8-II-77.

## LEUCTRIDAE

*Moselia infuscata* (Claassen).— NEVADA: Humboldt Co., Pine Forest Ra., Wood Canyon, 5 ♂ ♂, 9 ♀ ♀, 20-VI-77.

*Paraleuctra occidentalis* (Banks).— NEVADA: Elko Co., Jarbidge Mtns., Jacks Cr., ♂, 2 ♀ ♀, 11-VI-74; Ruby Mtns., Thomas Cr., ♂, 12-VI-74; White Pine Co., Schell Creek Ra., McCoy Cr., ♂, 5-V-77; Snake Ra., Lehman Cr., ♂, 3 ♀ ♀, 15-VI-74.

*Paraleuctra vershina* Gaufin and Ricker.— NEVADA: Elko Co., Jarbidge Mtns., Jarbidge R., ♂, ♀, 9-VI-74; Humboldt Co., Jackson Mtns., Bottle Cr., ♂ ♂, ♀ ♀, 19-VI-77; Santa Rosa Ra., Lye Cr., 5 ♂ ♂, 5 ♀ ♀, 19-VI-77; Sonoma Ra., Water Canyon, 3 ♂ ♂, 4 ♀ ♀, 18-VI-77; Lander Co., Toiyabe Ra., Big Cr., 2 ♂ ♂, 4 ♀ ♀, 24-VI-77; White Pine Co., Schell Creek Ra., McCoy Cr., 2 ♂ ♂, ♀ ♀, 26-VI-77; Snake Ra., Baker Cr., 2 ♂ ♂, 2 ♀ ♀, 13-VI-74.

## PELTOPERLIDAE

*Yoraperla brevis* (Banks).— NEVADA: Esmeralda Co., White Mtns., Middle Cr., ♂ ♂, ♀ ♀, 25-VI-77; Humboldt Co., Pine Forest Ra., Big Cr., 2 ♂ ♂, ♀, 19-VI-77.

## PTERONARCYIDAE

*Pteronarcella badia*? (Hagen).— NEVADA: Elko Co., Jarbidge Mtns., Bear Cr., nymph, 10-VI-74; Humboldt Co., Jackson Mtns., Trout Cr., nymphs, 5-IX-74, Pine Forest Ra., Wood Canyon, 2 ♀♀, 20-VI-77; Santa Rosa Ra., North Fork Little Humboldt R., nymphs, 4-II-77; Nye Co., Toiyabe Ra., Reese R., nymphs, 8-IX-74; White Pine Ra., Currant Cr., nymphs, 13-II-77; White Pine Co., Snake Ra., Snake Cr., nymphs, 14-II-77. The two females, and all the nymphs, appear to be the interior *P. badia* rather than *P. regularis* of the Cascades and Sierra Nevada. The two adult females were collected in the Pine Forest Ra. of northwestern Nevada where unequivocal Sierran species (*Moselia infuscata, Yoraperla brevis*) occur. The presence of apparent *P. badia* so far west suggests that the contact zone (Ricker 1964) of the *Pteronarcella* vicariants lies very close to the eastern front of the Sierra Nevada. Obviously more adult material is needed to substantiate this suggestion.

*Pteronarcys princeps* Banks.— Nevada: Elko Co., Jarbidge Mtns., Jarbidge R., nymphs, 9-VI-74; Esmeralda Co., Chiatovich Cr., nymphs, 10-II-77; Humboldt Co., Jackson Mtns., Bottle Cr., ♀, 19-VI-77; Pine Forest Ra., Big Cr., nymphs, 5-II-77; Santa Rosa Ra., Cabin Cr., nymphs, 26-IV-77; Sonoma Ra., Water Canyon, ♀, 18-VI-77; Nye Co., Toiyabe Ra., North Twin R., nymphs, 8-II-77; Pershing Co., Humboldt Ra., Star Cr., nymphs, 6-II-77; White Pine Co., Schell Creek Ra., Cleve Cr., nymphs, 16-II-77; Utah: Juab Co., Deep Creek Mtns., Trout Cr., nymphs, 15-II-77.

## PERLODIDAE

*Isoperla ebria* (Hagen).— Nevada: Humboldt Co., Sonoma Ra., Water Canyon, nymphs, 28-IV-77.

*Isoperla patricia* Frison.— Nevada: Humboldt Co., Pine Forest Ra., Alder Cr., 2 ♂♂, 20-VI-77; Nye Co., Toiyabe Ra., Peavine Cr., 1 ♂, 3 ♀♀, 24-VI-77; White Pine Ra., Currant Cr., nymphs, 13-II-77; White Pine Co., Schell Creek Ra., Kalamazoo Cr., 9 ♂♂, 3 ♀♀, 26-VI-77.

*Cultus* sp.— Nevada: Elko Co., Jarbidge Mtns., Jarbidge R., nymphs, 9-VI-74; Ruby Mtns., Lamoille Cr., nymphs, 17-II-77; Nye Co., Toiyabe Ra., South Twin R., nymphs, 1-V-77.

*Diura knowltoni* (Frison).— Nevada: Humboldt Co., Jackson Mtns., Bottle Cr., nymphs, 5-II-77; Santa Rosa Ra., Canyon Cr., nymphs, 4-II-77.

*Frisonia picticeps* (Hanson).— Nevada: Esmeralda Co., White Mtns., Middle Cr., nymphs, 2-V-77.

*Kogotus* sp.— Nevada: Esmeralda Co., White Mtns., Middle Cr., nymphs, 2-V-77.

*Megarcys signata* (Hagen).— Nevada: Elko Co., Jarbidge Mtns., Jacks Cr., nymphs, 11-VI-74; Ruby Mtns., Thomas Cr., nymphs, 12-VI-74; White Pine Co., Schell Creek Ra., McCoy Cr., 3 ♂♂, 3 ♀♀, 26-VI-77; Snake Ra., Lehman Cr., nymphs, 14-II-77.

*Skwala parallela* (Frison).— Nevada: Humboldt Co., Jackson Mtns., Bottle Cr., nymphs, 5-II-77; Santa Rosa Ra., North Fork Little Humboldt R., 2 ♂♂, 1 ♀, 26-IV-77.

## PERLIDAE

*Doroneuria baumanni*? Stark and Gaufin.— Nevada: Elko Co., Jarbidge Mtns., Snowslide Gulch, nymphs, 10-VI-74; Humboldt Co., Jackson Mtns., Bottle Cr., nymphs, 27-IV-77; Pine Forest Ra., Big Cr., nymphs, 27-IV-77; Santa Rosa Ra., Lye Cr., nymphs, 26-IV-77; Pershing Co., Humboldt Ra., Star Cr., nymphs, 6-II-77. Stark and Gaufin (1974) considered all Great Basin *Doroneuria* to be coastal *D. baumanni*. Adults of this late-emerging genus are needed to confirm the identity of the Jarbidge populations because Newell and Minshall (1976) reported both *D. baumanni* and interior *D. theodora* from southeastern Idaho.

*Hesperoperla pacifica* (Banks).— Nevada: Clark Co., Spring Mtns., Willow Cr., nymphs, 3-V-77; Elko Co., Jarbidge Mtns., Snowslide Gulch, nymphs, 10-VI-74; Humboldt Co., Jackson Mtns., Bottle Cr., ♀, 19-VI-77; Pine Forest Ra., Big Cr., ♂, 19-VI-77; Santa Rosa Ra., Canyon Cr., nymphs, 4-II-77; Lander Co., Toiyabe Ra., Kingston Cr., nymphs, 8-II-77; Nye Co., Quinn Canyon-Grant Ra., Troy Canyon, nymphs, 12-II-77; Pershing Co., Humboldt Ra., Buena Vista Cr., nymphs, 6-II-77; Sonoma Ra., Sonoma Canyon, nymphs, 6-II-77; White Pine Co., Schell Creek Ra., Kalamazoo Cr., nymphs, 16-II-77; Snake Ra., Baker Cr., nymphs, 13-II-77; White Pine Ra., White R., nymphs, 13-II-77; Utah: Juab Co., Deep Creek Ra., Granite Cr., nymphs, 15-II-77.

## CHLOROPERLIDAE

*Alloperla severa* (Hagen).— NEVADA: Humboldt Co., North Fork Little Humboldt R., ♂♂, ♀♀, 19-VI-77; White Pine Co., Schell Creek Ra., Kalamazoo Cr., 3 ♂♂, 1 ♀, 26-VI-77; White Pine Ra., Illipah Cr., 3 ♂♂, ♀, 13-VI-74.

*Suwallia pallidula* (Banks).—NEVADA: Humboldt Co., Santa Rosa Ra., North Fork Little Humboldt R., ♂♂, ♀♀, 19-VI-77; Nye Co., Toiyabe Ra., Peavine Cr., ♂♂, ♀♀, 24-VI-77.

*Sweltsa borealis* (Banks).— NEVADA: Humboldt Co., Jackson Mtns., Bottle Cr., 2 ♂♂, 3 ♀♀, 19-VI-77.

*Sweltsa coloradensis* (Banks).—NEVADA: Elko Co., Jarbidge Mtns., Canyon Cr., ♂, 11-VI-74; Humboldt Co., Pine Forest Ra., Big Cr., 10 ♂♂, 10 ♀♀, 19-VI-77; Santa Rosa Ra., Dutch John Cr., 3 ♂♂, 7 ♀♀, 19-VI-77; Sonoma Ra., Water Canyon, ♂♂, ♀♀, 18-VI-77; Nye Co., Currant Cr., 6 ♂♂, 3 ♀♀, 26-VI-77; White Pine Co., Schell Creek Ra., McCoy Cr., ♂♂, ♀♀, 26-VI-77.

*Sweltsa townesi* (Ricker).— NEVADA: Esmeralda Co., White Mtns., Middle Cr., 3 ♂♂, 3 ♀♀, 25-VI-77.

*Triznaka diversa* (Frison).— NEVADA: Esmeralda Co., White Mtns., Middle Cr., ♀, 25-VI-77.

*Triznaka pintada* (Ricker).— NEVADA: Humboldt Co., Jackson Mtns., Bottle Cr., ♂♂, ♀♀, 19-VI-77; Santa Rosa Ra., Cabin Cr., ♂♂, ♀♀, 18-VI-77; Sonoma Ra., Water Canyon, 2 ♂♂, ♀, 18-VI-77; Lander Co., Toiyabe Ra., Big Cr., 2 ♂♂, 24-VI-77; Nye Co., Quinn Canyon-Grant Ra., Cherry Cr., ♂♂, ♀♀, 25-VI-77; Pershing Co., Humboldt Ra., Star Cr., 3 ♂♂, 2 ♀♀, 18-VI-77; White Pine Co., White Pine Ra., Illipah Cr., 5 ♂♂, 3 ♀♀, 13-VI-74. Two forms differing in the shape of the female subgenital plate are present in this material. Specimens from northwestern Nevada are readily separable from those from the Toiyabe Ra. and eastern and southern ranges.

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## TABLE OF CONTENTS

Vegetative and edaphic factors affecting abundance and distribution of small mammals in southeastern Oregon. George A. Feldhamer ........ 207

Influence of precipitation and temperature on ring, annual branch increment, and needle growth of White Fir and Douglas-fir in central Utah. John D. Shane and Kimball T. Harper ........ 219

Studies in Nearctic desert sand dune Orthoptera, Part XVI: A new black *Stenopelmatus* from the Mescalero sands. Ernest R. Tinkham ........ 226

Potential use of Great Salt Lake water for lobster culture. Roger W. Mickelsen, Richard A. Heckmann, and Rex C. Infanger ........ 231

Nearctic stonefly genera as indicators of ecological parameters (Plecoptera: Insecta). Richard W. Baumann ........ 241

Competitive displacement as a factor influencing phytoplankton distribution in Utah Lake, Utah. Lorin E. Squires, Mark C. Whiting, Jack D. Brotherson, and Samuel R. Rushforth ........ 245

Ground nesting and aggressive behavior by the Swainson's Hawk (*Buteo swainsoni*). Neil D. Woffinden and James A. Mosher ........ 253

Response of reptile populations to different land management practices on the Idaho National Engineering Laboratory Site. Timothy D. Reynolds ........ 255

Decreases of juniper woodland in the Utah and Salt Lake valleys since settlement. E. M. Christensen and J. D. Brotherson ........ 263

Competition between harvester ants and rodents in the cold desert. Dan S. Landeen, Clive D. Jorgensen, and H. Duane Smith ........ 267

Food habits of burrowing owls in southeastern Idaho. R. L. Gleason and T. H. Craig 274

Flora of the Lee Creek valley, Alberta. R. Keith Shaw ........ 277

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*Subscriptions.* The annual subscription to the *Great Basin Naturalist* is $12 (outside the United States $13). The price for single numbers is $4 each. All back numbers are in print and are available for sale. All matters pertaining to the purchase of subscriptions and back numbers should be directed to Brigham Young University, Life Science Museum, Provo, Utah 84602. The *Great Basin Naturalist Memoirs* may be purchased from the same office at the rate indicated on the inside of the back cover of either journal.

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3-80 650 44539

ISSN 0017-3614

# The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 39 December 31, 1979 No. 4

## BORAGINACEAE OF THE SOUTHWESTERN UNITED STATES

Larry C. Higgins[1]

ABSTRACT.— The borage Family Boraginaceae is treated for the southwestern United States. Treated are 18 genera, 113 species, and 24 varieties from Arizona, New Mexico, and the desert regions of southeastern California. A key to the genera and species is included along with detailed descriptions, distribution data, chromosome counts when known, and comments for many of the taxa. A proposed new combination is *Plagiobothrys scouleri* (H. & A.) I. M. Johnston var. *cusickii* (E. L. Greene) Higgins.

This paper was prepared for the "Flora of the Southwestern United States," a project initiated by Dr. Noel H. Holmgren of the New York Botanical Garden and Dr. James Reveal of the University of Maryland. The project was funded by the National Science Foundation for a two-year period and then dropped. This paper was prepared during that interval.

The Family is both large and taxonomically complex. In the present treatment 113 taxa are recognized as occurring mainly in the states of Arizona and New Mexico, but also including the desert regions of southeastern California.

Generic limits within the family are fairly well defined; however, species are not so easily separated. The genus *Cryptantha* is such an example, in which both flowering and fruiting specimens are needed for precise identification. A more perplexing group is that of *plagiobothrys*, with its great variability in nutlet forms, flowers, and habitats that all run together, especially in the section allocarya. In the southwestern area the problems in the Boraginaceae are not as great as in other areas, such as the Great Basin and the coastal ranges of California.

Most borages are of little or no economic value, but form a very conspicuous part of the early spring flora throughout the southwest.

The following new combination in *plagiobothrys* is necessary at this time: *plagiobothrys scouleri* (H. & A.) I. M. Johnston var. *cusickii* (E. L. Greene) L. Higgins Comb. et. stat. nov., based upon *allocarya cusickii* Greene, pitt. 1:17, 1887.

### BORAGINACEAE

### Borage Family

Plants herbaceous, shrubby or arborescent, usually bristly hairy; *leaves* simple, alternate, or rarely opposite or whorled, entire, variously pubescent; *inflorescence* cymose, cymes glomerate, racemose or spikelike, frequently scorpioid and unilateral, usually bracteate; *calyx* usually deep 5-lobed or parted; *corolla* sympetalous, 5-lobed, regular or rarely somewhat irregular, sometimes crested with folds or saccate-intruded appendages (fornices) in the throat; *stamens* 5, borne on the corolla tube alternate with the lobes, included or less often exserted; *ovary* superior, 2-carpellate,

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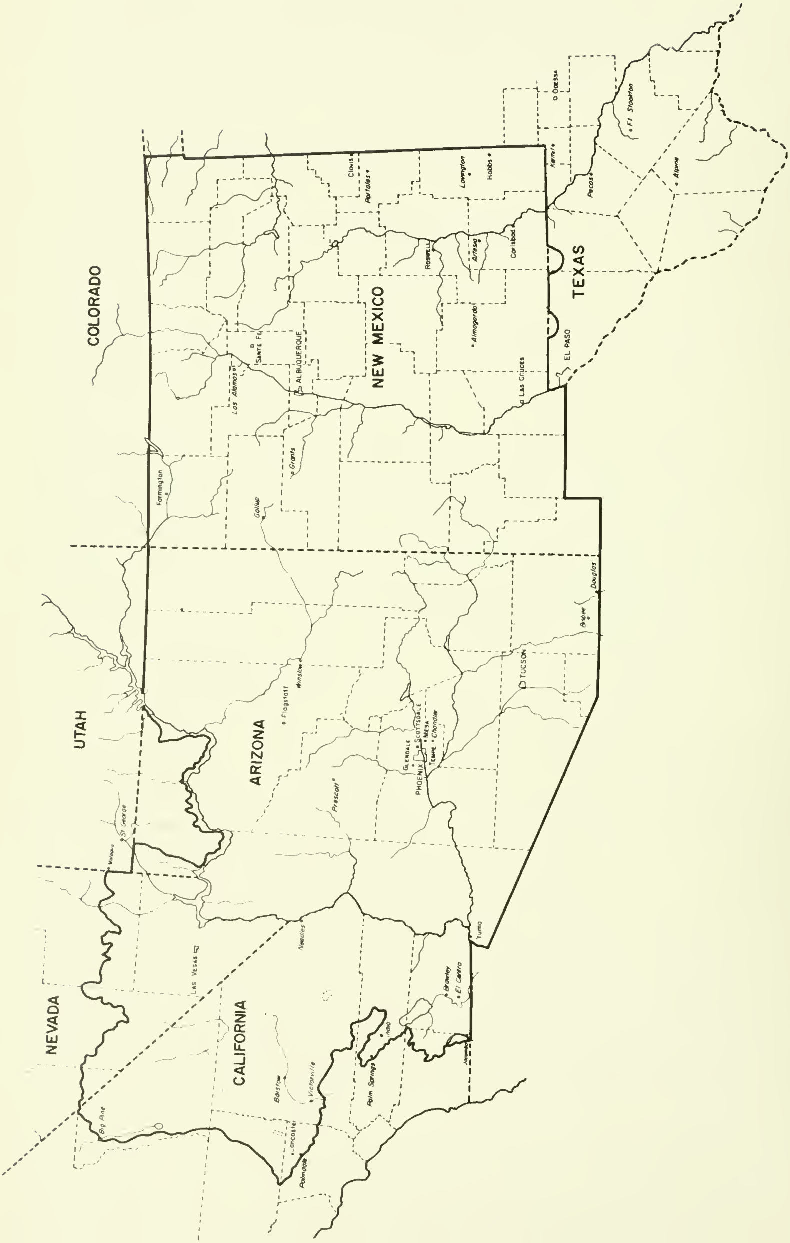
COLORADO
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CALIFORNIA
ARIZONA
NEW MEXICO
TEXAS
Farmington
Los Alamos
SANTE FE
ALBUQUERQUE
Grants
Gallup
Clovis
Portales
Lovington
Hobbs
Roswell
Artesia
Carlsbad
Alamogordo
Las Cruces
EL PASO
Odessa
Kermit
Pecos
Ft Stockton
Alpine
Douglas
Bisbee
TUCSON
Winslow
Flagstaff
Prescott
GLENDALE
PHOENIX
SCOTTSDALE
MESA
TEMPE
Chandler
Yuma
St George
Mesquite
LAS VEGAS
Needles
Brawley
El Centro
Indio
Palm Springs
Barstow
Victorville
Lancaster
Palmdale
Big Pine

Fig. 1. Area included in the treatment of the Boraginaceae of the Southwest.

usually 4-ovulate, entire or the carpels usually deeply 2-lobed, at maturity becoming tough and bony; *fruit* commonly breaking up into 4 simple-seeded mericarps (nutlets); *style* simple, entire or 2-lobed, produced from the pericarp at the apex of the fruit or borne between the nutlets on the receptacle, or on an upward elongation of the receptacle (gynobase); *endosperm* none or scarce; *embryo* straight or curved.

A family of about 100 genera and 2,000 species of worldwide distribution, with two principle centers of distribution; one about the Mediterranian region of the Mideast and the other in southwestern United States (Fig. 1).

The Boraginaceae are of little economic value, but some genera have numerous species that have been cultivated as ornamentals, principally in the genera *Myosotis* (forget-me-not), *Heliotropium* (heliotrope), *Anchusa*, and *Echium* (blue-weed).

The classification of the family is based primarily upon the characteristics of the fruit. In many cases it is nearly impossible to recognize the genus and species without the specimen having mature fruit.

1. Ovary entire or shallowly lobed, the style terminal .................... 2

— Ovary deeply 4-lobed, the style gynobasic .................... 4

2(1). Style twice cleft, the four branches each bearing a stigma .................... 1. *Cordia*

— Style cleft or divided once or simple or none .................... 3

3(2). Style distinctly cleft or divided to the base .................... 2. *Tiquilia*

— Style simple, very short, or absent .................... 3. *Heliotropium*

4(1). Stigma geminate or style bifid .................... 5

— Stigmas solitary and simple, capitate or disk-shaped .................... 8

5(4). Corolla irregular, oblique, stamens unequal .................... 4. *Echium*

— Corolla regular or nearly so, stamens equal .................... 6

6(5). Corolla large, 2.5–8 cm long, lobes acute; stamens very long, reaching at least to corolla sinuses and frequently much beyond .................... 5. *Macromeria*

— Corolla of small or medium size, less than 2.5 cm long; stamens very short, not equalling corolla sinuses .................... 7

7(6). Corolla lobes acute or acuminate, erect; style long, exserted, anthers sagittate .. .................... 6. *Onosmodium*

— Corolla lobes rounded or obtuse, ascending, spreading or recurved; style included or short exserted; anthers oblong .................... 7. *Lithospermum*

8(4). Nutlets attached near the apical end, widely spreading in fruit, armed with barbed or hooked prickles .................... 9

— Nutlets attached near base or middle, erect or parallel .................... 10

9(8). Nutlets subglobose, armed all over with barbed prickles; prickles; perennials; corolla usually blue or purplish .................... 8. *Cynoglossum*

— Nutlets flat, armed on the margins with hooked bristles; slender annuals; corolla white .................... 9. *Pectocarya*

10(8). Fruiting calyx distinctly irregular, three of the lobes nearly distinct, the other united enclosing the fruit, with 7–9 long glochidiate processes .................... .................... 10. *Harpagonella*

— Fruiting calyx regular or nearly so, not armed with glochidiate processes .................... 11

11(10). Corolla-lobes convolute in the bud; small herbs with usually ebracteate racemes and smoothly basally attached nutlets .................... 11. *Myosotis*

— Corolla-lobes imbricate in the bud .................... 12

12(11). Corolla bright yellow or orange, the throat open and not crested (with fornices) .......... 12. *Amsinckia*

— Corolla white or blue, sometimes light yellow; the throat usually crested .......... 13

13(12). Nutlets with definite medial ventral groove formed by the nonfusion of the pericarpial walls .......... 13. *Cryptantha*

— Nutlets with the pericarpial wall fused at least above the middle and commonly forming a medial ventral keel .......... 14

14(13). Dorsal surface of nutlets not encircled by an upturned rim or flange, with glochidiate appendages .......... 15

— Dorsal surface of nutlets encircled by an upturned rim or flange which is usually toothed or lacerate, commonly with uncinate hairs or glochidiate appendages .......... 16

15(14). Corolla white, throat very short and shallow, tube exceeded by or rarely just exceeding calyx; nutlets with a median dorsal keel; style usually shorter than nutlets .......... 14. *Plagiobathrys*

— Corolla blue, throat cylindrical or funnelform, tube usually much surpassing calyx; nutlets usually lacking a dorsal keel; style usually exceeding nutlets .......... 15. *Mertensia*

16(14). Nutlets not armed with conspicuous prickles, oblique, sometimes with a toothed rim or flange; low depressed pulvinate plants of high altitudes 16. *Eritrichium*

— Nutlets conspicuously armed with barbed prickles along the margins and also sometimes dorsally; plants with tall, well developed stems .......... 17

17(16). Annuals; pedicels erect in fruit; gynobase subulate, as long as the nutlets .......... 17. *Lappula*

— Perennials or biennials; pedicels recurved in fruit; gynobase broad and pyramidal, about half the length of the nutlets .......... 18. *Hackelia*

## 1. CORDIA L.

Trees or shrubs; *leaves* small to large, usually evidently petiolate, with entire, crenate or serrate margins; *inflorescence* mostly corymbose, ebracteate; *flowers* homomorphous or heterostyled or functionally more or less unisexual; *corolla* campanulate to funnel form, small to large, white, yellow, orange, or red, usually 5 merous; *stamens* exserted to included; *filaments* often hairy toward the base; *style* terminal on ovary, dichotomous, simple at the base, the two branches in turn forked to produce 4 ultimate branches; *stigmas* 4, clavate to spatulate or capitate; *fruit* a drupe with watery or glutinous mesocarp, or a nut; *endocarp* bony; *seeds* 1–4.

About 250 species of tropical or warm temperate areas, with the majority of the species and the greatest diversity in America.

### 1. **Cordia parvifolia** A. DC.

*Cordia parvifolia* A. DC. Prodromus 9: 498. 1845. (Coaguayanam, in western Michocán)

*Cordia greggii* Torr. Bot. Mex. Bound. 135: 1859. (The type probably came from near Mapimi, Durango, Mexico)

*Cordia watsoni* Rose, in Vasey & Rose, Contr. U.S. Natl. Herb. 1: 89. 1890. (*E. L. Palmer 174*, Guaymas, Mexico)

Shrub 1–3 m tall; *stems* with purplish black or dark gray bark, densely strigose when young but becoming glabrate with age, the lenticels small and pale gray; *leaves* obovate to ovate or nearly orbicular, serrate, 1–3 cm long, 3–15 mm wide, acute to rounded at apex, broadly cuneate at base, scabrous with short strigose hairs, pustulate at the base especially on the dorsal surface, veins conspicuous beneath, impressed above; *petioles* 2–10 mm long, slender; *inflorescence* cymose, few flowered, headlike; *calyx* tubular-campanulate, 5–8 mm long, 10-costate, abundantly hairy, grayish at base of tube, gradually becoming dark brown near and on the lanceolate teeth, the teeth 1.5–4 mm long; *corolla* white, thin, campanulate, 1.5–2.5 cm long, 1–3 cm broad, turning purplish or brownish in age; *style* heterostylous; *fruit* 6–9 mm broad, enclosed within the enlarging calyx.

Alluvial flats, rocky hillsides and wash bottoms in the lower sonoran zone. Extreme southern Arizona, south into Sonora, Coahuila, Durango, and Zacatecas, Mexico, and in central Baja California. February to November.

This shrubby borage is very common just to the south of our area in Mexico, but has only been collected once in the United States by *Altfillisch*, among *Larrea*, about 17 miles south of Tucson, Pima County, Arizona, in 1951.

## 2. TIQUILIA Pers.

Plants herbaceous or suffruticose; *stems* slender, forking, usually prostrate or widely spreading; *leaves* small, entire, usually strongly veined, subsessile or petiolate; *flowers* small, generally white, usually extra-axillary, along leafy twigs or at the forks of the branches, sometimes glomerate, commonly opening in late afternoon; *calyx* 5-parted, regular or slightly irregular; *corolla* with a short, cylindrical or ampliate tube and spreading lobes, throat naked or sometimes appendaged; *stamens* 4–5, included, their filaments adnate to the corolla-tube; *style* terminal on the ovary, short to long, bilobed or biparted; *stigmas* 2, not much differentiated from the style-branch; *ovary* 2-celled or sometimes 4-celled by the septumlike placentae, entire or 4-lobed; *fruit* dry, pyramidal or hemispheric, divided into usually 4 single-seeded nutlets; *nutlets* more or less broadly united ventrally or joined to the elongated gynobase.

### References

Johnston, I. M. 1961. Notes on some Texas Borages. Wrightia 2:156–162.

Lundell, C. L. 1964. Flora of Texas (Boraginaceae) 1(2):129–138.

Richardson, A. T. 1975. Monograph of the Genus Tiquilia. Unpublished dissertation Univ. of Texas.

1. Plant a small erect shrub; flowers and fruits aggregated into dense globose clusters terminating the leafy branches; *bracts* inconspicuous, simulating the filiform, plumose, elongate calyx lobes. .......... 1. *T. greggii*

— Plants low and spreading, usually prostrate; flowers and fruits borne in the leaf axils or mixed among the leaves in clusters borne along the branches .......... 2

2(1). Fruit nearly globose, unlobed at maturity, breaking apart into quarter-sections, each quarter forming a nutlet; *leaves* commonly with an ovate or eliptic blade; plant pallid, tomentose .......... 2. *T. canescens*

— Fruit deeply 4-lobed, the lobes joined only by their inner angle, each lobe forming a nutlet .......... 3

3(2). Leaves not evidently nerved, oblong to oblanceolate or linear, 1–2 mm broad, setose, base of petiole expanded, indurate, usually villous .......... 4

— Leaves with evident impressed nerves, ovate or obovate to nearly orbicular, strigose or merely short-hispid; base of petiole not expanded or indurate or villous .......... 6

4(3). Corolla bud bearing abundant minute stipitate glands, otherwise glabrous; attachment-scar on nutlet entirely closed or opened only above the middle .......... 3. *T. gossypina*

— Corolla bud villulose, or rarely also sparsely glanduliferous; attachment-scar of nutlets opened for its entire length, or at least below the middle .......... 5

5(4). Leaf 5–17 mm long, 1.1–4.2 mm broad, blade obovate to narrowly obovate, petiole densely ciliate; nutlet obpyriform to ovoid, 1.5–2.0 mm long .................. 4. *T. latior*

— Leaf 4–8 mm long, 0.5–2 mm broad, blade linear to narrowly obovate, petiole not noticeably ciliate, nutlet ovoid, 1–1.5 mm long .......................... 5. *T. hispidissima*

6(3). Plants annual; corolla pink or white; sepals with short pungent hairs; style shorter than calyx .......................... 6. *T. nuttallii*

— Plants perennial; corolla blue or bluish; sepals villous; style longer than the calyx .......................... 7

7(6). Leaves with about 6 pairs of deeply impressed veins; calyx long-villous within; nutlets elongate .......................... 7. *T. plicata*

— Leaves with only 2–3 pairs of shallowly impressed veins; calyx glabrous or short pubescent within; nutlets nearly globose .......................... 8. *T. palmeri*

1. **Tiquilia greggii** (Torr. & Gray) A. Richardson

*Ptilocalyx greggii* Torr. & Gray Pacif. R. R. Reports 2: 110. 1857. *Coldenia greggii* A. Gray, Synop. Fl. N. Amer. 2: pt. 1. 182. 1878. *Tiquilia greggii* A. Richardson sida 6(3):336. 1976. (*Gregg*, near Buena Vista, Mexico)

Usually a small, erect, rounded shrub 2–5 dm tall; *stems* or old branches decidedly fruticose, the twigs pale and hispidulous or tomentose; *leaves* numerous, ovate or elliptic, 5–9 mm long, 2.5–6 mm broad; thickish, usually veinless, the margin revolute, the surfaces densely tomentulose; *flowers* in dense capitate clusters 1–2 cm in diameter, borne terminally on the leafy stems and uppermost branchlets; *bracts* inconspicuous, filiform, plumose, like the calyx-segments; *calyx* sessile, deciduous, 5–9 mm long, the segments filiform, plumose, unequal, purplish or grayish at maturity; *corolla* pink, densely villous in the bud, 6.5–8 mm long, the lobes rounded, 2–3.5 mm broad; *style* 2.5–3.2 mm long, slender, the lobes 0.5–0.8 mm long, persistent on the mature fruit; *fruit* lance-ellipsoidal, 2–2.5 mm long, 1–1.2 mm broad, thin-walled, by abortion always 1-celled and 1-seeded, dorsal surface shiny, sparsely hispidulous above the middle, ventral surface dull, the papery tissue representing the three aborted cells of the fruit.

Widely distributed on limestone soils. Southern New Mexico in the Organ Mountains, western Texas and southward in eastern Chihuahua, western and southern Coahuila, to northern Zacatecas and Durango. May to October.

This plant is a Calciphile and usually restricted to limestone soils. It enters our area only along the southern boundary in extreme southern New Mexico.

2. **Tiquilia canescens** (DC.) A. Richardson

*Coldenia canescens* DC. Prodromus 9: 559. 1845. *Stegnocarpus canescens* Torr. in Torr. & Gray Pacif. R. R. Reports 2: 170. 1857. *Tiquilia canescens* A. Richardson, sida 6(3): 236, 1976. (*Berlandier* 2256, between Santander and Victoria, Mexico)

*Stegnocarpus leiocarpa* Torr. in Torr. & Gray Pacif. R.R. Reports 1: 320. 1855. (Pecos River Valley of the Rio Grande, Texas)

*Coldenia canescens* var. *subnuda* I. M. Johnst. Proc. Calif. Acad. Sci. Ser. 4. 12: 1137. 1924. (*I. M. Johnston 3731*, San Nicolas Bay, Lower California)

*Coldenia canescens* var. *pulchella* I. M. Johnst. J. Arnold Arbor. 20: 379. 1939. *Tiquilia canescens* var. *pulchella* (I. M. Johnst.) A. Richardson. sida 6(3):236. 1976. (*F. Shreve* 6257, Kofa Mountains, Arizona) = var. pulchella

Suffrutescent perennial, often forming mats 2–6 dm in diameter; *stems* numerous, mostly prostrate but sometimes ascending, furcately branched, older stems with exfoliating epidermis, rough, dark colored, leafy stems and branches pallid, tomentose; *leaves* numerous, white tomentose, the petiole slender, 2–7 mm long, at extreme maturity usually breaking off near the middle leaving a stub attached to the stem, the blade ovate to elliptic-lanceolate, obtuse to broadly acute at both ends 7–10(15) mm long. 2–7(9) mm broad, thickish, the margins somewhat revolute; *flowers* usually solitary in the leaf axils and along the main stem and branches; *calyx* sessile, persistent, at anthesis 3–4 mm long, in fruit becoming 4–8 mm long, the segments lanceolate with long-attenuate tips; *corolla* 5–6(12) mm in total length, pink, rose, or white, the lobes broad and rounded, 1.8–3(4.5) mm wide, 1.5–2(3.5) mm long, usually villous in the bud, margins frequently erose; *style* seated in the pericarp at the apex of the fruit, persistent, 1.5–2.5 mm long; *fruit* at maturity ovoid or globose, glabrous or hairy, 2.5–3 mm in diameter, 2–2.5 mm high, not lobed; *nutlets* bony, densely and minutely tuberculate.

Rocky ridges, hillsides, and bajadas, mostly on limestone soils below 4,000 feet elevation; lower sonoran life zone. Southeastern California and southern Nevada, east to southwestern Utah, through Arizona and New Mexico into Texas and south through most of the desert area of Mexico. March to May.

Plants from south of our range tend to have pubescent fruits, while those in our range tend to have glabrous fruits; however, there seems to be no geographical correlation, so is not recognized nomenclaturally. Variety *pulchella* (Johnston), Richardson seems to be worthy of at least some recognition, as it can be separated from typical material by the larger flowers 9–12 mm long, 5–8 mm wide, and by the bluish or lavender rather than white corolla. This variety is best developed in the Kofa Mountains of Arizona and just west into California in the Chocolate and Chuckwalla mountains.

3. **Tiquilia gossypina** (Woot. & Standl.) A. Richardson

*Eddya gossypina* Woot. & Standl. Contr. U.S. Natl. Herb. 16: 164. 1913. *Tiquilia gossypina* A. Richardson sida 6(3):236. 1976. (*E. O. Wooton*, Tortugas Mountains southwest of Las Cruces, Dona Ana County, New Mexico. September 2, 1894).

Plant prostrate, forming mats 2–4 dm broad; *stems* numerous, dichotomously branched, when young densely villulose; *leaves* somewhat cinereous, clustered, borne mostly on very short branchlets along the main stem, the petiole triangular or ovate, 1.5–2 mm long, indurate, the blade oblong or oblanceolate, 4–8 mm long, 1–2 mm wide, in age detaching from the persistent petiole, upper surface hispid, pustulate, also finely villulose, lower surface only partially covered by the revolute leaf margins, midrib prominent, villulose-hispidulous; *flowers* borne in the leaf clusters, the bud minutely stipitate glandular, otherwise glabrous; *calyx* at anthesis 3–3.5 mm long, sessile, persistent, the segments lanceolate, short villous or hispidulous; *corolla* pink to magneta, 7–8 mm long, the lobes rounded, 2.5–3 mm broad; *style* somewhat compressed, 3–3.5 mm long, the two lobes each 0.6–0.8 mm long; *fruit* ovoid or globose, 0.9–1.5 mm high, covered with grayish papillae; *nutlets* bony, dusky, papillate, the scar closed or narrowly open only above the middle.

Growing in gypsum soils on desert flats and slopes, 4,000 feet elevation or lower. Dona Ana County, New Mexico, south and eastward along the Rio Grande Valley into Trans-Pecos Texas and Chihuahua and western Coahuila Mexico. April to October.

This plant is closely related to *T. hispidissima* from farther north, but with no evidence of hybridizing between the two species.

4. **Tiquilia latior** (I. M. Johnst.) A. Richardson

*Goldenia hispidissima* var. *latior* I. M. Johnst. Contr. Gray Herb. 68: 92. 1923. *Tiquilia latior* A. Richardson sida 6(3):236. 1976. (*Kennedy* & *Goodding* 79, Muddy Valley, Lincoln County, Nevada)

Plants prostrate perennials, forming mats 2–6 dm in diameter; *stems* numerous, dichotomously branched, spreading from a woody taproot, the younger branchlets villulose-hispidulous; *leaves* clustered, borne mostly on very short branchlets along the main stem, the petioles 1–2 mm long, broadest (1–1.5 mm) at the base, becoming indurate, usually pallid, the margin hispid-ciliate, the blade usually obovate (rarely ovate or elliptic), 5–17 mm long, 1.1–4.2 mm wide, usually broader than the petiole; *flowers* borne among the leaves; *calyx* sessile, broadly and permanently attached in the leaf axil, at anthesis 2.5–3.5 mm long, the segments lanceolate, united at the base, villulose-ciliate below the middle, frequently terminated with a stiff bristle; *corolla* usually pink, 4–8 mm long, 4–5 mm broad, the lobes rounded, spreading; *style* 1.5–2.2 mm long, somewhat flattened, apex bilobed; *fruit* ovoid; *nutlets* oblong-ovoid, usually only 1 or 2 maturing, 1.5–2.0 mm long, papillate or vesicular papillate, scar open, nearly as long as the nutlet, surrounded by a nonpapillate ridge.

Sandy dunes and dry open slopes or on gypsum flats, mostly below 5,000 feet elevation. Central Utah and Arizona.

5. **Tiquilia hispidissima** (T. & G.) A. Richardson

*Eddya hispidissima* T. & G., Senate Executive Doc. No. 78, 33 Congr., 2nd session vol. 2:170, 171. plate 8. 1857. *Coldenia hispidissima* Gray, Proc. Amer. Acad. Arts 5:340. 1862. *Tiquilia hispidissima* A. Richardson sida 6(3):236. 1976. (Wright 1557, common on the Rio Grande about El Paso, 1852)

Plants prostrate perennials forming mats to 6 dm in diameter; *stems* numerous, dichotomously branched, spreading from a woody taproot. The young branchlets hispidulous-appressed; *leaves* clustered, on short brittle branches, the petioles very short, elliptic or somewhat rectangular, glabrous, with pungent bristles along the margins, the blade linear or narrowly lanceolate, 4–8 mm long, 0.5–2 mm broad; *flowers* axillary, solitary; *calyx* sessile at anthesis 2.5–3.5 mm long, the segments narrowly triangular or subulate, united at the base, ciliate or villous with scattered sharp bristles; *corolla* usually pink 2.5–6.5 mm long, 4–5 mm broad, the lobes rounded, spreading; *style* 1.5–4.2 mm long, cleft at the apex; *fruit* ovoid; *nutlets* ovoid, 1–1.5 mm long.

Occurring mainly on gypseous soils, or occasionally calcareous soils in central New Mexico and Trans-Pecos Texas.

This plant is closely allied to *T. latior* from farther west in Utah and Arizona, but is distinguished from that taxa by its linear leaves, less ciliate petioles, and smaller ovoid, white colliculate nutlets.

6. **Tiquilia nuttallii** (Benth. ex. Hooker) A. Richardson

*Coldenia nuttallii* Hook. J. Bot. Kew Gard. Misc. 3: 296. 1851. *Tiquiliopsis nuttallii* A. A. Heller, Muhlenbergia 2: 239. 1906. *Tiquilia nuttallii* A. Richardson sida 6(3):236. 1976. (*Geyer 80.* Utah, Utah Co., Sandy desert of muddy rivers edge near the Great Salt Lake timpanogos, Aug. 1845)

*Tiqulia brevifolia* Nutt. ex Torr. Bot. Mex. Bound. 136. 1859. (*Schott*, desert west of the Colorado, California, March)

Prostrate annual herb forming mats 1–3.5 dm broad; *stems* slender, dichotomously branched, somewhat brittle, finely strigose; *leaves* ovate to nearly suborbicular, 4–8 mm long, narrowly revolute, often hispid on the margins, dorsal surface with 2–3 pairs of distinct veins, hirsute, ventral surface thinly strigose with impressed veins, the petioles slender, usually as long or longer than the blade; *flowers* in compact clusters in the forks and at the ends of the branchlets; *calyx* sessile, 4–5 mm long, the segments linear-subulate, villous or setulose on the back, the margins sparsely but conspicuously hispid; *corolla* pink or nearly white, 3–4 mm long, the limb 2–2.5 mm broad, the tube with 5 triangular scales near the base; *style* about 1 mm long; *fruit* ovate-ovoid; *nutlets* oblong-ovoid, smooth and shiny, somewhat mottled with brownish patches, scar closed or narrowly linear.

Dry sandy or alkaline plains and hillsides, up to 7,000 feet elevation. Eastern Washington to California on the eastern slope of the Sierra Nevada Mountains eastward to Wyoming, Utah, and Arizona, also in Argentina. May to August.

7. **Tiquilia plicata** (Torr.) A. Richardson

*Tiquilia brevifolia* var. *plicata* Torr. Bot. Mex. Bound. 136. 1859. *Coldenia plicata* Coville, Contr. U.S. Natl. Herb. 4: 163. 1893. *Tiquilia plicata* A. Richardson sida 6(3):237. 1976 (Lt. Emory sn. desert west of the Colorado, California)

Matted perennial from a deep woody root; *stems* several, freely dichotomously branched, the branches puberulent or glabrate; *leaves* obovate, 4–9 mm long, densely hairy with felt-like grayish pubescence, strongly plicate, the ventral surface with 4–7 pairs of deeply impressed veins, the petioles about as long as the blade; *flowers* clustered in the forks and at the ends of the branchlets; *calyx* 2–3 mm long, the segments subulate, tomentose especially inside; *corolla* 4–6 mm long, 2–3 mm broad, bluish or lavender; *style* about 2 mm long, cleft ½ to ¾ of its total length; *fruit* ovoid; *nutlets* ovoid, 1–3 usually maturing, about 1 mm long, smooth, shiny, the scar orbicular.

Sandy desert flats and bajadas in the *Larrea-Ambrosia* association, mostly below 3,000 feet elevation. Southern California and Northern Mexico eastward to southern Nevada and western Arizona. April to July.

8. **Tiquilia palmeri** (A. Gray) A. Richardson

*Coldenia palmeri* A. Gray, Proc. Amer. Acad. Arts 8: 292. 1879. *Coldenia brevicalyx* S. wats. Proc. Amer. Acad. Arts. 24: 62. 1889. *Tiquilia palmeri* A. Richardson sida 6(3):236. 1976. (*E. Palmer*, southeastern California, Arizona, on the lower Colorado, 1869)

Prostrate or ascending perennials 1–3 dm tall, or forming mats 2–10 dm broad; *stems* many, dichotomously branched from the woody root, white-barked, with the bark exfoliating in age; *leaves* obovate to ovate, grayish strigose to setulose, 4–9 mm long, 3–5 mm wide, the blade equal to or occasionally much shorter than the petiole, which is 3–11 mm long, irregularly veined with 2–3 pairs of moderately impressed veins; *calyx* 2–3.5 mm long, ovate, the segments linear-subulate, villulose; *corolla* lavender, 5–7 mm long, 5–6(8) mm broad; *style* 3–4 mm long, cleft about half its length; *fruit* ovoid; *nutlets* subglobose, ca. 1 mm long, smooth, shiny, 1 or more usually aborted.

Sandy places usually below 500 feet elevation. Southeastern California and western Arizona to northern Mexico, along the Colorado River to above Needles.

A plant closely allied with *T. plicata* but easily recognized by the leaves with 2–3 pairs of impressed veins.

## 3. HELIOTROPIUM L.

### Heliotrope

Annual or perennial, herbaceous or more or less shrubby plants; *stems* erect or ascending to nearly prostrate, glabrous to pubescent; *leaves* small to large, sessile or petiolate; *inflorescence* unilateral and generally conspicuously scorpioid, with or without bracts; *calyx* 5-lobed; *corolla* white, yellow, or purple, variable in form, the throat frequently pubescent inside; *anthers* included; *filaments* extremely short; *style* present or absent; *stigma* usually frustrumlike or conic, mostly sterile, receptive only in a band around the base; *fruit* dry, at maturity breaking up into 4 single-seeded or 2 2-seeded nutlet.

A genus of about 250 species widely scattered throughout the warmer parts of the world. They are particularly abundant in arid regions. (Greek, helios, sun, and trope, turning, referring to the summer solstice when the species were supposed to come into flower.)

### Reference

Ewan, J. A. Review of the North American weedy Heliotropes. Bull. So. Calif. Acad. Sci. 41: 51–57. 1942.

1. Plant very succulent, glabrous, usually glaucous ............................ 1. *H. curassavicum*
— Plant not succulent, hairy, never glaucous ............................................................ 2
2(1). Plant perennial, rhizomatous, the parts above the ground renewed annually ..... ........................................................................................ 2. *H. greggii*
— Plant annual ................................................................................................ 3
3(2). Corolla 8–15 mm wide, with a long-exserted tube; style elongate, many times longer than the stigma ............................................................ 3. *H. concolvulaceum*
— Corolla 2–4 mm wide, usually with an included tube; style short, about as long as the stigma ........................................................................... 4. *H. fruticosum*

## 1. **Heliotropium curassavicum L.**

*Heliotropium curassavicum* L. Sp. Pl. 1: 130. 1753. (Curacao, in Dutch West Indies)

*H. xerophyllum* Cockrell, Bot. Gaz. 33: 379. 1902. *H. curassavicum* var. *xerophyllum* Nels. & Macbr. Bot. Gaz. 61: 35. 1916. (*D. A. Cockrell*, East Las Vegas, New Mexico, 3 December, 1901) = var. *curassavicum*.

*H. curassavicum* var. *obovatum* A. DC. Prodromus 9: 538. 1845. (*Douglas*, Columbia River) = var. *obovatum*.

*H. spathulatum* Rydb. Bull. Torrey Club 30: 262. 1903. (*R. S. Williams 542*, Great Falls, Montana = var. *obovatum*.

*H. oculatum* A. Heller, Muhlenbergia 1: 58. 1904. *H. curassavicum* var. *oculatum* I. M. Johnst. ex Tidestr. Proc. Biol. Soc. Wash. 48: 42. 1935. *H. spathulatum* subsp. *oculatum* Ewan, Bull. S. Calif. Acad. Sci. 4: 56. 1942. (*A. A. Heller 5813*, sand along the Russian River at Healdsburg, Sonoma County, California) = var. *oculatum*.

Annual or short-lived perennial herbs; *stems* branched, prostrate or decumbent, succulent or rubbery, glabrous, frequently glaucous, 1–6 dm long; *leaves* oblanceolate to obovate or spathulate, glabrous, thick and succulent, 1–4 cm long, 3–20 mm broad, apex obtuse to acutish; *inflorescence* terminal or extra-axillary and lateral along the leafy stems, cymes scorpioid, single or paired, densely flowered, in fruit elongating, 6–12 cm long; *bracts* lacking; *calyx* parted to near the base, sessile, the segments lanceolate to oblong, equal, fleshy, at anthesis 1–3 mm long, slightly accrescent in fruit; *corolla* white or bluish, the throat often with a violet purple eye, 1.5–3.5(5) mm long, 3–15 mm wide, the limb ascending or loosely outcurved; *stigma* conic, obscurely 4-lobed at apex; *fruit* subglobose, obscurely didymous, separating into 4 nutlets.

Sandy to clayey alkaline soils along beaches, near ponds, streams, playa lakes or similar areas. Throughout the United States and south into Mexico, widely distributed on all continents.

*H. curassavicum*, in our flora, can be divided into three varieties with some consistency by the following key.

1. Plant scarcely glaucous, slender, only slightly succulent; leaves narrowly oblanceolate to linear; calyx less than 2 mm long, spreading; corolla 1–2.5 mm long, mostly in southern and eastern New Mexico .................................... var. *curassavicum*

— Plants conspicuously glaucous, thickish, usually very succulent; leaves obovate or broadly oblanceolate; calyx over 2 mm long, the lobes erect; corolla 2.5 mm or longer .................................................................................................... 2

2(1). Corolla 5–9(16) mm broad, at most only purplish-tinged at the throat; fruit 2.5 mm wide; northern New Mexico, rare ....................................... var. *obovatum* A. DC.

— Corolla 3–5(7) mm broad, usually becoming distinctly purple or purplish at the throat; fruit 1.5–2 mm wide; southeastern California, southern Nevada and western Arizona ............................................ var. *oculatum* I. M. Johnston ex Tidestr.

2. **Heliotropium greggii** Torr.

*Heliotropium greggii* Torr. Bot. Mex. Bound. 137. 1859. (*Gregg*, Valley of Conchos, near Santa Rosalia, Chihuahua, Mexico, May)

*H. palmeri* A. Gray ex S. Wats. Proc. Amer. Acad. Arts. 18: 121. 1883. (*E. Palmer 891*, 892, at Soledad, Coahuila, Mexico)

Plants perennial, arising from a deep rhizome; *stems* numerous, prostrate or loosely decumbent, ascendingly branched, 5–15 cm long, strigose with closely appressed hairs; *leaves* numerous, thickish, lanceolate to linear, strigose, 10–25(30) mm long, 2–5 mm wide, midrib conspicuous but veins absent, margins revolute; *inflorescence* at first glomerate, then elongating into a unilateral cyme 10–50 cm long, 5- to 10-flowered; *bracts* few and inconspicuous; *calyx* 5-lobed, 2–3 mm long, the segments lanceolate, strigose; *corolla* white with a yellow eye, fragrant, the tube 3–5 mm long, the limb 7–12 mm broad; *style* short about 1 mm long, puberulent, the tip bidentate; *fruit* radially 4-lobed, very pubescent, 3 mm wide, 1.5 mm high, usually 4 nutlets maturing.

Frequent along roadsides and in bar ditches, in sand, gravel, or clay soils, usually forming colonies where water collects temporarily. Southeastern New Mexico, Trans-Pecos Texas, and south through Coahuila and eastern Chihuahua to northern Zacatecas and northeastern Durango, Mexico. April to September.

3. **Heliotropium convolvulaceum** (Nutt.) A. Gray

*Batschia albiflora* Raf. New. Fl. N. Amer. pt. 4: 19. 1836. non *H. albiflorum* Engelm. 1924. *Euploca albiflora* I. M. Johnst. Contr. Gray Herb. 70: 53. 1924. (*Nuttall*, Arkansas River, on sand bars)

*Euploca convolvulaceum* Nutt. Trans. Amer. Philos. Soc. 5: 190. 1837. (*Nuttall*, sandy banks of the Arkansas)

*E. grandiflora* Torr. in Emory, Notes Mil. Reconn. 147. 1848. (*Emory*, Rio Grande below Santa Fe, New Mexico)

*Heliotropium californicum* E. L. Greene, Bull. Calif. Acad. Sci. 1: 202. 1885. *H. convolvulaceum* var. *californicum* I. M. Johnst. Contr. Arnold Arbor. 3: 83. 1932. *Euploca albiflora* var. *californica* Jeps. & Hoover in Jepson, Fl. Calif. 3: 299. 1943. (*Mrs. Curran*, Mohave Desert, June 1884)

Erect annual 1–4 dm tall; *stems* simple below, branched above with ascending branches, strigose to spreading hispid; *leaves* numerous, the blade lanceolate to ovate, 10–45(50) mm long, 4–15(20) mm broad, entire, apex acute, strigose to hispid, the petiole slender 3–8 mm long; *flowers* extra-axillary, borne along the leafy branches; *bracts* leaflike, numerous; *calyx* in anthesis 4–6 mm long, in fruit becoming 6–8 mm long, the segments linear-lanceolate, slightly unequal, strigose or appressed setose; *corolla* white with a yellow throat, fragrant, the tube 8–12 mm long, strigose outside, the limb broadly funnelform, 15–22 (30) mm wide, not lobed, pentagonal, plicate in the bud; *style* slender, 3–4 mm long; *fruit* laterally compressed, hairy, 2-lobed, 3–4 mm long; nutlets paired.

An abundant plant especially on sand dune areas or sandy soils. California eastward to Utah, Wyoming, and Nebraska and southward into Chihuahua Mexico. June to December.

The morning glory heliotrope is a very striking and handsome plant especially in late summer and fall when it covers low sandy areas. In California and western Arizona a phase of the species has conspicuous spreading setose or hispid pubescence. This is variety *californicum* (E. L. Greene) Johnston.

### 4. **Heliotropium fruticosum** L.

*Heliotropium fruticosum* L. Syst. Nat. ed. 10. 913. 1759. (Browne, Jamaica)

*H. phyllostachym* Torr. Bot. Mex. Bound. 137. 1859. (Santa Cruz, Sonora, Mexico)

Annuals; *stems* sparingly branched from the base and above, spreading-ascending, 0.5–2.5(4) dm long, strigose with whitish hairs; *leaves* elliptic to oblanceolate, 1–2(3.5) cm long, 2–7 mm broad, acute to rounded at apex, broadly cuneate at the base, strigose, midribs producing coarser hairs with pustulate bases, dark green above, paler beneath, the margin narrowly and tightly revolute; *inflorescence* spikelike; *flowers* extra axillary; *bracts* leaflike, conspicuous; *calyx* elliptic, 1–1.5 mm long in anthesis, the segments narrowly ovate-lanceolate, unequal, strigose and somewhat pustulate; *corolla* small, white, the tube 1–1.5(2.5) mm long, the limb 3–4 mm wide, finely strigose on the outside, also papillate; *style* 0.6–0.8 mm long; *fruit* depressed-globose, puberulent with fine white hairs, 1.2–1.5 mm high; *nutlets* rounded on the back, brownish, lateral faces each bearing a central pit.

Sandy to rocky slopes, ridges and wash bottoms, 5,000 feet elevation or less. Colombia and Venezuela northward in the West Indies and Central America to Mexico and southern Arizona in the United States.

## 4. ECHIUM L.

### Blueweed

Plants biennial or possibly perennial; *stems* erect, hispid; *leaves* alternate, entire; *inflorescence* of a series of sympodial scorpioid cymes which are usually bracteate; *calyx* 5-parted; *corolla* blue to violet purple, irregular, tubular-funnelform; *fornices* lacking, the throat thus open; *stamens* unequally exserted on the corolla, the longer ones surpassing the corolla; *style* exserted from the corolla, 2-cleft at apex; *gynobase* flat or nearly so; *nutlets* erect, rugose, attached at their bases, the scar large and sometimes surrounded by a low rim.

A genus of about 50 species native to Europe, the Mediterranean region, South Africa, and the Atlantic islands. (From Greek echion, name for several members of the Boraginaceae, echion, in turn, comes from echis, viper.)

### 1. **Echium vulgare** L.

*Echium vulgare* L. Sp. pl. 139. 1753. (Europe)

Plants biennial or short-lived perennials; *stems* erect, usually solitary, (2)4–6(10) dm tall, hispid, the hairs often pustulate; *leaves* mostly basal, reduced upward, oblanceolate to linear oblong, the cauline sessile, setose-hirsute, also finely tomentose, 3–15(22) cm long, 8–15(35) mm broad; *inflorescence* virgate, elongate, occupying most of the stem cymose-paniculate with numerous, aggregated scorpioid cymes 2–5 cm long; *bracts* conspicuous, lanceolate to ovate-lanceolate 0.5–3 cm long; *pedicels* short, 1 mm or less long; *calyx* 5–6 mm long in anthesis, in fruit becoming 6–9 mm long, setose-hirsute; *corolla* 10–15(20) mm long, irregular, bright blue, pubescent externally; *fornices* lacking, the tube open; *stamens* conspicuously exserted from the corolla; *style* exserted, hairy, 17–20 mm long; *nutlets* about 3 mm long, rugose. N = 18, 16.

Roadsides, fields, and waste places; native of southern Europe, now widely introduced in the eastern United States and westward to Washington, Colorado, and New Mexico. June to September.

*Echium vulgare* is known from our area only by a single collection made by Cockerell at Mesilla, New Mexico.

### 5. MACROMERIA Don.

Plants erect, abundantly rough-hairy, usually branched near the base; *stems* usually several from the branched caudex, abundantly pubescent; *leaves* lanceolate to obovate, entire, strongly veined; *flowers* in terminal leafy-bracted, scorpioid racemes, whitish, greenish-white or yellowish; *calyx* deeply 5-parted; *corolla* much surpassing the calyx, trumpet shaped, the lobes erect or recurved, ovate, acute; *stamens* just surpassing the corolla lobes to long exserted, the versatile anthers oblong, obtuse, the filaments elongate-filiform; *ovary* 4-lobed; *style* exserted from the corolla tube, enlarged and persistent at the base; *nutlets* ovoid to globular, usually all 4 maturing.

A genus containing about 8 species in Mexico and southwestern United States.

1. **Macromeria viridiflora** DC.

*Macromeria viridiflora* DC. Prodromus 10: 68. 1846. (In Mexico)

*Onosmodium thurberi* A. Gray, Synop. Fl. N. Amer. 2: pt. 1 205. 1878. *Macromeria thurberi* Mack. Bull. Torrey Club 32: 496. 1905. (*Thurber, Bigelow* & *Wright*, New Mexico)

Plants erect perennials; *stems* several, branched only from the base, 3–10 dm tall, setose-hispid with spreading bristles 2–3 mm long; *leaves* at base oblanceolate, the upper ones becoming lanceolate to elliptic, sessile, entire, strongly veined, 3–10(15) cm long, (6)10–23 mm broad, grayish pubescent with spreading setose hairs; *calyx* in fruit 13–17(20) mm long, setose, the segments linear; *corolla* trumpet shaped, greenish yellow, 40–50 mm long, canescent, the lobes ovate, erect, 4–5 mm long; *stamens* barely exserted; *filaments* flattened, elongate; *anthers* versatile, 3–4 mm long, oblong; *style* tardily elongating, inconspicuously geminate, exceeding the corolla lobes 5–10 mm; *nutlets* ovoid, to nearly globose, smooth or slightly pitted, all 4 maturing.

Open or wooded areas in the higher mountains, 6,000 to 10,000 feet elevation. Eastern Arizona and western New Mexico, south into Mexico. July to September.

It is reported that the Hopi Indians used a mixture of this plant with tobacco in their "rain bringing" ceremony.

### 6. ONOSMODIUM Michx.

Plants rough-hairy perennial herbs; *stems* erect or ascending, several branched from the base; *leaves* largely or nearly all cauline, alternate, entire, strongly veined; *inflorescence* 5-parted, the segments unequal, narrow, sometimes disarticulating at the base; *corolla* white or yellow, tubular, slightly enlarged at the throat, 5-lobed, glabrous within, more or less hairy outside, the lobes erect, acute or acuminate, the sinuses inflexed; *fornices* lacking; *stamens* 5, included; *style* exserted; *nutlets* globular, 4 mm long or less, smooth or sometimes sparingly pitted, broadly attached at the base to the depressed gynobase, commonly only 1 or 2 maturing.

A genus consisting of about 5 species in the United States and Canada. (Named for its resemblance to *Onosma*, an old world genus of the Boraginaceae)

#### Reference

Mackenzie, K. K. Onosmodium. Bull. Torrey Club 32: 495–506. 1906.

1. **Onosmodium molle** Michx.

*Onosmodium molle* Michx. Fl. Bor. Amer. 1: 133. 1893. *Lithospermum molle* Muhl. Cat. pl. 19: 1813. *Purshia mollis* Lehm. Asperif. 383. 1818. *O. carolinianum* var. *molle* A. Gray, Synop. Fl. N. Amer. 2 pt. 1: 206. 1878. (About Nashville, Tennessee)

*Onosmodium occidentale* Mack. Bull. Torrey Club. 32: 502. 1905. *O. molle* var. *occidentale* I. M. Johnst. Contr. Gray Herb. n. s. 70: 18. 1924. (Numerous specimens are cited from Canada to Texas)

Perennial herbs; *stems* several arising from a woody root, branching above or often from the base, erect, 3–6(12) dm tall, coarsely and loosely pubescent throughout; *leaves* 4–8 cm long, 10–20 mm broad, acutish, prominently 5–7 nerved on both surfaces, strigose or spreading setose, minutely pustulate on the ventral surface; *bracts* leaflike, often 2-rank-ed, 10–24 mm long; *calyx* 6–12 mm long, the segments lanceolate-linear, acute, setose with spreading bristles; *corolla* greenish white, 12–20 mm long, canescent on the outside, the acute lobes 3–4 mm long; *style* exceeding the corolla lobes 5–10 mm; *nutlets* ovoid, acutish, 3.5–4 mm long, dull, smooth, little if at all pitted.

In open rocky woods, prairies, wastelands, and moderately dry hillsides. United States and adjacent Canada from the Appalachian Mountains to the Rocky Mountains and south into New Mexico and Texas. March to July.

In the past monographers have recognized *O. molle, occidentale, bejariense, helleri, hispidissimum,* and *subsetosum* as distinct species; however, I believe that these represent weak variants of the same species. In our flora only the variety *occidentale* occurs, this phase just entering northeastern New Mexico in Union County.

## 7. LITHOSPERMUM L.

### Puccoon

Plants annual or perennial, herbaceous or fruticose; *stems* usually erect, 1 to several, simple below, branched above, often dye stained at the base; *leaves* alternate; *inflorescence* racemose, bracteate; *calyx* 5-parted, the lobes usually narrow; *corolla* white, yellow, or violet, tubular or salverform, tube cylindrical, the imbricate lobes spreading, the throat with fornices or with pubescent or glandular areas; *stamens* included, affixed in the tube; *filaments* short; *anthers* oblong; *style* filiform; *stigmas* geminate; *nutlets* 4, or rarely less by abortion, erect, ovoid or angular, smooth or verrucose; *gynobase* broadly pyramidal or flat.

A genus consisting of about 60 species, mostly North American with about 20 species of the old world. A purple dye was obtained from the roots of many species by the North American Indians.

### Reference

Johnston, I. M. Studies in the Boraginaceae XXIII. A survey of the genus *Lithospermum*. J. Arnold Arb. 33: 299–363. 1952.

1. Stems arising out of a basal cluster of leaves, the largest leaves at the base of the stem .................... 2

– Stems arising from a bud on a caudex, root-crown, or rhizome, the largest leaves usually on the midstem, the lowest leaves scalelike and very reduced .................... 5

2(1). Flowers heterostylic, none cleistogamic; corolla usually about as broad as long, funnelform, the throat unappendaged but conspicuously stipitate-glandular, the tube villous inside; plant spreading by rhizomes .................... 1. *L. cobrense*

– Flowers monomorphic, sometimes cleistogamic; corolla usually longer than broad, salverform, the throat with fornices, only sparsely stipitate-glandular, the tube glabrous inside; plant with a taproot .................... 3

3(2). Corolla-lobes erose or fimbriate; fruiting calyx usually drooping or nodding; nutlets smooth or somewhat pitted; cleistogamous flowers very abundant .................... 2. *L. incisum*

– Corolla-lobes with entire margins; fruiting calyx erect .................... 4

4(3). Nutlets roughened, strongly verrucose or rugose; chasmogamic flowers abundant, large .................... 3. *L. parksii*

– Nutlets smooth and shiny; chasmogamic flowers few or none, plant commonly almost completely cleistogamic .................... 4. *L. confine*

5(1). Flowers heterostylic; corolla tube not narrowly constricted at top .................... 5. *L. multiflorum*

– Flowers not heterostylic; corolla tube cylindrical, elongate, narrowly and distinctly constricted at the top .................... 6. *L. viride*

### 1. Lithospermum cobrense E. L. Greene

*Lithospermum cobrense* E. L. Greene, Bot. Gaz. 6: 157. 1881. (*E. L. Greene*, Santa Rita del Cobre)

Plant perennial, stoloniferous, forming colonies; *stems* erect, simple, 2–6 dm tall, strigose to somewhat setose; *leaves* at base of plant withering before anthesis, oblanceolate, 5–10 cm long, 5–16 mm broad, the cauline leaves very numerous, crowded, much smaller than the basal ones, narrowly oblong to linear, obtuse, sessile, 1–3.5(5) cm long, 2–5 mm broad, the margins loosely revolute; *inflorescence* scorpioid, simple or geminate, loosely flowered, racemes 10–20 cm long at maturity; *bracts* conspicuous; *calyx* at anthesis 5–7 mm long, in fruit becoming 6–10 mm long, the segments linear-oblong, unequal, strigose; *pedicels* 3–5 mm long in fruit, much shorter in flower; *corolla* funnelform, pale yellow, the tube 7–9 mm long, villous inside, stipitate glandular, the limb (12)15–20 mm broad, margins entire; *style* heteromorphic, 2–8 mm long; *nutlets* white, lustrous, plump, smooth or sometimes obscurely tuberculate, 2.5–3 mm long.

Dry to moderately moist openings in oak or pine forests, 5,000 to 10,000 feet elevation. Southern Arizona and New Mexico east to western Texas and south in the mountainous areas of Chihuahua and Durango, Mexico. June to August.

### 2. Lithospermum incisum Lehm.

*Lithospermum angustifolium* Michx. Fl. Bor. Amer. 1: 130. 1803. non Forsk 1775. *Cyphorina angustifolia* Nieuwl. Amer. Mid. Nat. 3: 194. 1914. (Ohio River)

*Batschia longiflora* Pursh. Fl. Am. Sept. 132. 1814. *Lithospermum longiflorum* Spreng. Syst. 1: 544. 1825. non Salisb. 1796. *Pentalophus longiflorus* A. DC. Prodromus 10: 86. 1846. (*Nuttall*, banks of the Missouri.)

*Lithospermum incisum* Lehm. Asperif. 303. 1818. (Missouri)

*Batschia decumbens* Nutt. Gen. pl. 1: 114. 1818. *Lithospermum mandanense* Spreng. Syst. 1: 544. 1825. *Pentalophus mandanense* A. DC. Prodromus 10: 87. 1846. *Cyphorina mandanense* Nieuwl. Amer. Midl. Nat. 4: 515. 1916. non *Lithospermum decumbens* Vent. 1800. (*Nuttall*, Fort Mandan on the Missouri)

*Lithospermum linearifolium* Goldie, Edinb. New Philos. Journal 6: 322. 1822. (Head of Lake Ontario)

*Lithospermum breviflorum* Engelm. & A. Gray, Journ. Bost. Soc. N. H. 5: 252. 1845. (*Lindheimer* 278, clay prairie near Industry, Austin County, Texas. 1844)

*Lithospermum cryptanthiflorum* Brand, Feddes Repert. Spec. Nov. Regni Veg. 28: 13. 1930. (Bourgeau, Winnipeg Valley. 1859)

Plant perennial, from a stout woody taproot; *stems* clustered, 0.5–3(6) dm tall, strigose or occasionally weakly setose; *leaves* mostly cauline, the lowermost reduced and chaffy or rarely developed and oblanceolate, the other linear-oblong to narrowly lanceolate, loosely revolute, numerous, 2–6 cm long, (1)2–4(6) mm wide; *inflorescence* racemose, the flowers extra-axillary, those developing early in the season showy, yellow, well developed; *bracts* very conspicuous; *calyx* 5–12 mm long in fruit, the segments linear, very unequal; *pedicels* recurving in fruit; *corolla* salverform, yellow, the tube 12–30(40) mm long, the limb 10–15(20) mm wide, the lobes erose or fimbriate; *style* heteromorphic, 5–30 mm long; *nutlets* ovate, with a conspicuous ventral keel, 3–3.5 mm long, gray, shiny, sparsely pitted, the scar sunken and bearing a nearly central projection that is attached by a ridge to the dorsal part of the prominent collar. N = 12.

Widely distributed in various habitats, but usually in sandy or gravelly soils along roadsides, on prairies or in wasteland. In the United States chiefly on the Great Plains and along the Rocky Mountains, but extending westward into Arizona and Nevada, north into Canada and south into Mexico. March to August.

Flowers developing early in the season are very showy with long styles; however, they are nearly always sterile. Those developing later in the growing season are cleistogamous, mostly fertile, and with short styles.

### 3. Lithospermum parkii I. M. Johnston

*Lithospermum parksii* I. M. Johnst. J. Arnold Arbor. 33: 345. 1952. (*R. McVaugh 7725*, Devils Lake, about 20 miles north northwest of Del Rio, Val Verde County, Texas)

Plant perennial, with a deep, thick, somewhat woody taproot; *stems* erect or ascending, 2–5(6) dm tall, simple or several, weakly setose with spreading pubescence; *leaves* at base of stem 5–9 cm long, 4–13 mm broad, oblanceolate, obtuse at apex, usually drying up by anthesis, the cauline leaves numerous, linear to oblance-linear, gradually reduced in size; *inflorescence* terminal and extraaxillary, scorpioid, the racemes unilateral and 10–20 cm long; *bracts* conspicuous; *calyx* at anthesis

4–12 mm long, in fruit 9–15 mm long, the segments linear; *pedicels* 1–5 mm long; *corolla* salverform, yellow, the tube 5–17 mm long, the limb (7)12–20 mm broad, the tube finely strigose on the outside, the lobes entire; *fornices* conspicuous, 0.5–0.8 mm long, invaginate, sparsely glandular; *style* slender and elongate, 4–15 mm long; *nutlets* opaque, verrucose or rugulose, about 3 mm long, attachment scar triangular, about 1.7 mm broad.

Rocky open ridges and slopes mostly on exposed limestone soils. Eddy County, New Mexico, in the Guadalupe Mountains, south through western Texas into northern Chihuahua, Mexico. March to August.

*L. parksii* is principally a species which occurs to the south and east of our range. Our plants belong to variety *parksii*, but variety *rugulosum* Johnston is a more southerly ranging plant of Coahuila and Nuevo León, Mexico. This plant is small and less robust with smoother, shiny nutlets.

4. **Lithospermum confine** I. M. Johnston

*Lithospermum confine* I. J. Johnst. J. Arnold Arbor 33: 346–347. 1952. (*Mueller 2378*, Canyon de los Capulines, about San Enrique, Hacienda San José de Raices, Nuevo León, Mexico, 6 August 1935)

Plants perennial; *stems* several, erect, strigose, 2–4 dm tall; *leaves* at base oblanceolate, obtuse at apex, 2–6 cm long, (1)3–10 mm wide, strigose, cauline leaves lanceolate to linear, the margin narrowly revolute; *inflorescence* terminal, at maturity the racemes 5–10 cm long; *bracts* conspicuous; *calyx* at anthesis 4–5 mm long, in fruit becoming 6–10 mm long, the segments linear; *pedicels* erect, 2–10 mm long; *corolla* yellow, *chasmogamic flowers* with the corolla tube 7–10 mm long, the limb 5–6 mm wide, the lobes entire; *fornices* trapeziform, invaginate, slightly glanduliferous; *style* 5–10 mm long; *cleistogamic flowers* inconspicuous 1–3 mm long, style 1.5–3 mm long; *nutlets* whitish, smooth, 3–3.5 mm long, 2–2.5 mm wide, smooth, the base more or less constricted.

Dry open slopes, canyons, to moderately moist oak and evergreen woodlands. Southern New Mexico and Arizona south into western Texas, and Coahuila, to Neuvo León, Mexico. April to July.

5. **Lithospermum multiflorum** Torr. in A. Gray

*Lithospermum multiflorum* Torr. in A. Gray, Proc. Amer. Acad. Arts 10: 52. 1874. (No type indicated, originally given as from "Colorado in the lower mountains, to New Mexico and Texas")

Plant perennial; *stems* erect, 1 to several, 2–5 dm tall, simple or late in season ascendingly branched, pubescence thin, grayish, strigose, frequently pustulate; *leaves* at the base poorly developed, ovate to lanceolate, scalelike, acute, 3–10 mm long, usually dye stained, the cauline gradually becoming larger and better developed, sessile, lanceolate to lance-linear, 2–7 cm long, 3–9 mm wide; *inflorescence* simple or forked, terminal on the stem and branches, 5–15 cm long at maturity, late in season producing some very fertile cleistogamic flowers; *calyx* of normal flowers 4–6 mm long at anthesis, the segments linear, very unequal, in fruit becoming 6–10 mm long; *pedicels* in anthesis 1–3 mm long, in fruit 3–8 mm long; *corolla* orange-yellow, the tube 8–10 mm long, limb 8–9 mm broad; *fornices* very obscure, these and the throat conspicuously stipitate glandular; *style* 3–9 mm long, heterostyled; *nutlets* ovoid, white or brownish, usually smooth 2.5–3.5 mm long, 2–2.5 mm wide, usually only one maturing.

Widely distributed in the mountains, 5,000 to 10,000 feet elevation, mostly in open areas on sandy or gravelly soils. Eastern Utah and northern Arizona, east to Colorado and south through New Mexico, and western Texas into the mountainous areas of Chihuahua, Mexico. June to October.

6. **Lithospermum viride** E. L. Greene

*Lithospermum viride* E. L. Greene, Bot. Gaz. 6: 158. 1881. (*E. L. Greene*, Mimbres Mountains near Georgetown, Grant County, New Mexico. 1877)

*L. palmeri* S. Wats. Proc. Amer. Acad. Arts 18: 122. 1883. (*E. Palmer 903*, Sierra Madre, south of Saltillo, Coahuila, Mexico)

Plant perennial; *stems* few to numerous, 2–10 dm tall, simple or loosely ascendingly branched, pubescence of two kinds, the more abundant spreading or retrorsely appressed, the less abundant spreading and ascending, more rigid and shorter; *leaves* all cauline, the basal third of stem with scalelike leaves that are 3–20 mm long, the largest leaves near the middle of the stem, 2–5.5(8) cm long, 8–32 mm broad, the blade elliptic to lance-ovate, with an evident midrib and 1 or more pairs of prominent veins, the upper surface dark green, scabrous, pustulate, lower surface velvety strigose and paler; *inflorescence* simple or forked, terminal on the stems, in age elongating, loosely flowered, 10–30 cm long; *bracts* leaflike; *flowers* all monomorphic; *calyx* at anthesis 8–13 mm long in fruit becoming 10–18 mm long, the segments linear, very unequal; *pedicels* in anthesis 1–2 mm long in fruit 3–10 mm long; *corolla* greenish yellow, pubescent externally, with a large cylindrical tube 10–30 mm long, limb small reflexed; *fornices* lacking, but abundantly glanduliferous in the throat; *style* slender and elongate 10–30 mm long; *nutlets* ovoid, plump, white or brownish, smooth or obscurely pitted, 3.5–4.5 mm long, 2.7–3 mm broad.

Usually on limestone soils in the mountainous areas, 6,000 to 10,000 feet elevation. Arizona and southern New Mexico, southeast through Trans-Pecos Texas and Coahuila into the mountains of Nuevo Leon, Mexico. June to September.

### 8. CYNOGLOSSUM L.

### Hound's Tongue

Plants biennial or perennial rarely annual; *stems* mostly tall, erect, commonly coarse and pubescent; *leaves* alternate, the basal ones long petioled, the upper sessile; *inflorescence* elongating, racemose, bractless or bracted only at the base; *calyx* 5-parted, to below the middle, spreading or reflexed and somewhat accrescent at maturity; *corolla* funnelform or salverform, purple, blue, or white, the tube short, the lobes broad, spreading imbricate, the throat closed by the 5 fornices; *stamens* included; *filaments* short; *anthers* oblong or elliptic; *nutlets* 4, depressed-ovoid or orbicular, glochidiate, ascending or divaricate, attached above the middle.

A cosmopolitan genus of about 75 species. (Greek kuno, dog, and glossa, tongue, because of leaf texture in some of the species)

1. **Cynoglossum officinale L.**

*Cynoglossum officinale* L. Sp. pl. 134. 1753. (Europe)

Biennial; *stems* stout, erect, 4–5 dm tall, leafy to the top, villous-tomentose throughout; *leaves* at base of plant oblong to oblong-lanceolate, 15–30 cm long, 2–7 cm wide, the upper leaves lanceolate, acute or acuminate, sessile or clasping; *inflorescence* racemose, the racemes several to many, simple or branched, much elongating in fruit; *bracts* evident or lacking; *calyx* 5–7 mm long in fruit, the segments ovate-lanceolate, obtuse to acutish, villous-strigose; *pedicels* 5–12 mm long; *corolla* reddish purple to blue, the broad tube 3–5 mm long, the limb 6–8 mm broad; *style* subulate, 4–5 mm longer than mature fruit; *nutlets* ascending on the pyramidal gynobase, 5.5–6 mm long, flattish on the upper surface and margined, glochidiate all over, splitting away from the gynobase at maturity but hanging attached to the subulate style.

Dry to somewhat moist open areas in mixed evergreen or oak woodlands, 5,000 to 9,000 feet elevation. Native to Europe and Asia, now widely introduced in the United States westward to Montana, Utah, and Arizona. May to July.

### 9. PECTOCARYA DC ex. Meisn.

Small annual herbs; *stems* slender, spreading; *leaves* linear, with closely appressed strigose hairs; *inflorescence* a series of leafy-bracteate false racemes which constitute most of the plant; *calyx* 5-parted, the narrow lobes spreading or reflexed in fruit; *corolla* white, the tube shorter than the calyx, the lobes ovate, the throat nearly closed by the 5 fornices; *stamens* included; *style* very short; *stigma* capitate; *nutlets* 4, flattened, attached above the middle, obovate-spathulate to nearly linear, spreading, usually paired, mostly margined with hooked hairs that are spreading or recurving; *gynobase* broadly pyramidal.

About 10 species of western North America and western South America. (From the Greek pektos, combed, and karyon, nut, from the row of bristles on the margin of the nutlet.)

1. Nutlets orbicular or nearly so, both the body and the very thin conspicuous wing with slender uncinate bristles ........................................ 1. *P. setosa*
— Nutlets oblong or linear, the body without uncinate bristles ........................................ 2
2(1). Nutlets with the margins pectinately lacerate or toothed most of their length, also commonly uncinate-bristly near the distil end ........................................ 3
— Nutlets with the margins entire or undulate, armed only at the distil end where densely uncinate-bristly ........................................ 5
3(2). Nutlets conspicuously recurved; the margin narrow with nearly distinct teeth .. ........................................ 2. *P. recurvata*
— Nutlets nearly straight ........................................ 4
4(3). Margin of nutlets broad and conspicuous, the teeth confluent .......... 3. *P. platycarpa*
— Margin of nutlets narrow, the teeth usually not confluent ........................ 4. *P. linearis*
5(2). Nutlets all winged margined ........................................ 5. *P. penicillata*
— Nutlets heteromorphic, 1 of each divergent pair wingless, or merely margined, the other with a broad somewhat incurved uncinate-toothed wing ..................... ........................................ 6. *P. heterocarpa*

1. **Pectocarya setosa** A. Gray

*Pectocarya setosa* A. Gray. Proc. Amer. Acad. Arts 12: 81. 1876. *Gruvelia setosa* Rydb. Bull. Torrey Club 40: 479. 1913. (*E. Palmer*, southeastern California on the desert plains of the upper Mohave River)

*P. setosa* var. *aptera* I. M. Johnst. Contr. Gray Herb. 70: 38. 1924. (*L. Abrams 3671*, Campo, San Diego County, California)

*P. setosa* var. *holoptera* I. M. Johnst. Ibid. 70: 39. 1924. (*I. M. Johnston 6489*, Granite Well, Mohave Desert, California)

*Stems* usually simple at base, but branched just above with ascending branchlets, 5–20 cm tall, setose with spreading bristlelike hairs, also thinly strigose; *leaves* linear to linear-oblanceolate, 5–20 mm long; *calyx* 3–4 mm long in fruit, the segments narrowly linear, armed with 3–6 straight divergent bristles; *nutlets* divergent in pairs, broadly obovate to orbicular, 2 of them bordered all around with a thin scarious wing, 2 wingless, the body and usually the wings producing slender uncinate bristles, the wing usually slightly undulate and slightly curved upward and saucerlike.

Dry, usually sandy or gravelly slopes, hillsides or flats, up to 7,000 feet elevation. Eastern Washington and Idaho, south through western Utah, Nevada, and Arizona to southern and lower California. April to June.

2. **Pectocarya recurvata** I. M. Johnston

*Pectocarya recurvata* I. M. Johnst. Contr. Arnold Arbor. 3: 97. 1932. (*Harrison & Kearney 6507*, near Chandler, Maricopa County, Arizona, 26 March 1930)

*Stems* slender, diffusely branched from the base, the branches ascending, 5–25 cm long, sparsely strigose with closely appressed hairs; *leaves* linear to narrowly lance-linear, 1–3.5 cm long, 0.5–2 mm broad, acute, strigose or weakly setose, pustulate on the dorsal surface; *calyx* 2–3 mm long in fruit, the segments linear-lanceolate, strigose; *nutlets* divergent in pairs, linear, strongly recurved at full maturity, the wing divided to or almost to the body into prominent subulate straw-colored uncinate bristles, at the apex the wing prolonged into a short scarious tip, uncinate bristly on the margin.

Dry, sandy to gravelly slopes and mesa below 4,000 feet elevation. Southeastern California and Baja California, Mexico eastward to southern Nevada, southern Utah, Arizona, Hildago County, New Mexico, and south into Sonora, Mexico. March to April.

This delicate little plant is readily recognized because of its strongly recurved nutlets.

3. **Pectocarya platycarpa** (Munz. & Johnst.) Munz. & Johnst.

*Pectocarya gracilis* var. *platycarpa* Munz. & Johnst. Contr. Gray Herb. 70: 36. 1924. *P. platycarpa* Munz. & Johnst. Contr. Gray Herb. 81: 81. 1928. (*Pringle*, Mesas near Camp Lowell, Arizona, 16 April, 1881 in part)

*Stems* slender, diffusely branched from the base, prostrate or widely ascending, 5–20(37) cm long, strigulose; *leaves* narrowly linear to linear-oblanceolate, 1–3.5 cm long, 0.5–1.5 mm broad, cinereous-strigulose, acute; *calyx*

3–4 mm long in fruit, the segments linear-oblong, strigose, nearly as long as the nutlets; *nutlets* divergent in pairs, sometimes heteromorphous, linear-oblong to spathulate-oblong, 2.5–3(4) mm long, with a broad conspicuous winged margin bearing irregular uncinate teeth, the odd nutlet, when present, with a more deeply lacerate wing, and a more pubescent body.

Dry, gravelly or sandy mesas or bajadas or rocky hillsides usually below 4,000 feet elevation. Baja California, Mexico, and southeastern California eastward through southern Nevada into southwestern Utah, Arizona, southern New Mexico and extreme western Texas, El Paso County, and south into Sonora, Mexico. March to April.

4. **Pectocarya linearis** (R. & P.) DC.

*Pectocarya linearis* var. *ferocula* I. M. Johnst. Contr. Arnold Arbor. 3: 95. 1932. (*Munz & Crow 11846*, Lady Harbor, Santa Cruz Island, California)

*Stems* slender, diffusely branched from the base, the branches prostrate to ascending, 8–25 cm long, strigose; *leaves* linear, 0.5–2.5 cm long, 0.5–1.5 mm broad, acute, strigose; *calyx* 1.5–2.5 mm long in fruit, the segments linear; *nutlets* divergent in pairs, 3–4 mm long, linear-oblong, the winged margin very narrow and producing 5–8 small, narrowly subulate, nearly distinct uncinate bristly teeth on each side, the body nearly straight, not recurved.

Dry, sandy, or gravelly slopes mostly below 4,000 feet elevation. Islands off the coast of southern California and on the mainland from Monterey County south to Baja California, Mexico, also South America in the dry arid regions. March to May.

*P. linearis* var. *ferocula* is the North American phase of the species. Although it is closely allied to the South American plant, the nutlets of var. *ferocula* tend to be monomorphic with slightly broader based teeth than in the typical material.

This plant is extremely rare in our flora, entering only near the extreme western boundary on the foothills of the San Bernardino Mountains, at the desert edge, and Kern County near Mohave.

5. **Pectocarya penicillata** (H. & A.) A. DC.

*Cynoglossum penicillatum* H. & A. Bot. Beechey Voy. 371. 1840. *Pectocarya penicillata* A. DC. Prodromus 10: 120. 1846. *P. linearis* var. *penicillata* M. E. Jones, Proc. Calif. Acad. Sci. 5: 709. 1895. (*Douglas*, California)

*Stems* many, diffusely branched from the base, prostrate or widely ascending, 5–15(25) cm long, cinereous-strigose; *leaves* linear, 1–2(3) cm long, 0.5–2 mm broad, setose-strigulose, pustulate on the dorsal surface; *calyx* 1.5–2 mm long in fruit, the segments linear, nearly as long as nutlets; *nutlets* divergent in pairs, monomorphous, oblong, 1.6–2.4 mm long, the margin unequal, upturned and incurved, broadest near the base and apex, subentire and armed only at the apex with uncinate-bristles, all the bristles slender and not dilated near the base.

Dry, sandy or gravelly hillsides, slopes or mesas, usually below 4,500 feet elevation. British Columbia and eastern Washington, south to southern California and eastward through Idaho to western Wyoming, and Arizona. February to June.

6. **Pectocarya heterocarpa** (I. M. Johnst.) I. M. Johnston

*Pectocarya penicillata* var. *heterocarpa* I. M. Johnst. Contr. Gray Herb. 70: 37. 1924. *P. heterocarpa* I. M. Johnst. J. Arnold Arbor. 20: 399. 1939. (*Munz & Keck 4870*, Corn Springs, Chuckwalla Valley, Riverside County, California)

*Stems* slender, diffusely branched from the base, ascending or spreading, 5–15(25) cm long, strigose; *leaves* narrowly linear, 1–3 cm long, 0.5–2 mm broad canescent-strigulose, commonly pustulate on the dorsal surface; *calyx* 1.5–2 mm long in fruit, the segments narrowly lanceolate to elliptic; *nutlets* about 2 mm long, heteromorphic, divergent, 2 narrower and with or without a narrow-winged margin, and 2 with prominently winged margins, the wings uncinate bristly mostly at the apex, irregular, few toothed and with or without scattered bristles on the sides.

Dry, sandy, or gravelly bajadas or mesas mostly below 3,000 feet elevation. Southern California and Baja California, Mexico, eastward to southwestern Utah, extreme western Texas in El Paso County, and south into Sonora, Mexico. February to April.

## 10. HARPAGONELLA A. Gray

Small pubescent annual; *stems* branching from near the base, prostrate or ascending; *leaves* linear-lanceolate or linear, canescent;

*inflorescence* racemose, floriferous to near the base of the stem, subbracteate; *calyx* unequal, 3 of the lobes distinct, the other 2 fused, the whole accrescent and closely enclosing the fruit, armed with 5–9 soft hooked spines; *corolla* white, minute; *style* entire; *nutlets* 1 or 2 dissimilar, thin-coreaceous, smooth to finely muriculate, obliquely attached by the narrow base; *gynobase* depressed, small.

A monotypic genus of southwestern United States and northern Mexico. (Name diminutive of Latin harpago, grappling hook.)

1. **Harpagonella palmeri** A. Gray

*Harpagonella palmeri* A. Gray, Proc. Amer. Acad. Arts 11: 88. 1876. (*E. Palmer*, Guadalupe Island, off Lower California, 1875)

*Stems* slender, diffusely branched from the base, nearly prostrate to ascending, 4–30 cm long; *leaves* linear or narrowly lanceolate, acute, 1–3.5 cm long, 1–3 mm broad, strigose, the dorsal surface evidently pustulate; *calyx* segments 1–1.5 mm long in anthesis, in fruit becoming 2–3.5 mm long; *pedicels* short, stout, recurving in fruit; *corolla* white, minute, 1.5–2 mm long; *nutlets* about 3 mm long, one enclosed in the indurate calyx tube, the other free, minutely muricate to nearly smooth, often covered with small trichomes.

Dry, sandy to gravelly mesas and bajadas mostly below 1,700 feet elevation. Los Angeles County to San Diego County and Baja California, Mexico, eastward to southwestern Arizona and Sonora, Mexico. February to April.

Rare and local species, usually occurring only during favorable years with sufficient moisture for good seed germination. A very unusual borage because of the highly modified assymetrical calyx which resembles a grappling hook.

## 11. MYOSOTIS L.

### Forget-me-not

Annual or perennial herbs; *stems* slender, usually erect; *leaves* alternate, entire; *inflorescence* racemose, bracted or bractless; *calyx* 5-parted, cut to beyond the middle into lanceolate or triangular lobes; *corolla* blue, white, or rarely pink, the tube short, salverform, the throat with prominent fornices; *stamens* adnate to the corolla tube, included or exserted; *nutlets* 4, small, ovoid, smooth and shiny, sharply margined, the attachment scar flat; *gynobase* short and depressed.

A genus of about 30–35 species widely distributed in the temperate regions of the world. (From the Greek, mus, mouse, and otos, ear, because of appearance of the leaves of some species.)

1. **Myosotis scorpioides** L.

*Myosotis scorpioides* L. Sp. pl. 131. 1753. (Europe)
*M. scorpioides* var. *palustris* L. Ibid. *M. palustris* Lam. Fl. France 2: 283. 1778. (Europe)

Fibrous rooted perennial herbs; *stems* 2–6 dm tall, often creeping at the base, commonly stoloniferous as well, strigose; *leaves* oblong to oblanceolate, sessile, 2–8 cm long, 7–15(20) mm broad, obtuse; *inflorescence* terminal, the racemes usually in pairs, becoming loose and open; *bracts* lacking; *calyx* in anthesis 1.5–2.5 mm long, in fruit becoming 3–5 mm long, the segments triangular, short, strigose, equalling or shorter than the tube; *pedicels* in fruit spreading, 4–7 mm long; *corolla* blue with a yellow eye, tube short about 2 mm long, the limb 5–8(10) mm broad; *nutlets* angled, keeled on the inside, smooth. N = 32.

In shallow water or moist places. Native of Europe, now widely distributed in North America as an escapee from cultivation.

*Myosotis scorpioides* was reported in Kearney and Peebles in *Arizona Flora*. They noted that the species had been planted in gardens around Flagstaff and that it may become naturalized in that area of our flora.

## 12. AMSINCKIA *Lehm.*

### *Fiddleneck*

Taprooted, bristly-hairy annuals; *stems* usually simple below, branched above; *leaves* alternate, linear to ovate, entire; *inflorescence* racemose, scorpioid, usually bractless; *calyx* cleft to the base or nearly so, or some of the lobes connate so as to appear if fewer than 5 segments; *corolla* bright yellow or orange, tubular or salverform, glabrous, the throat without fornices; *stamens* included, the filaments short; *nutlets* 4, erect, angulate-ovoid, with a conspicuous ventral keel extending from the tip to near the middle or below, often somewhat keeled dorsally also, the scar small and placed at the end of the ventral keel, often elevated and carunclelike; *gynobase* short pyramidal.

A genus of about 15 species of western North America and South America. (Named for William Amsinck, burgomaster of Hamburg and patron of its botanical garden during the early part of the 19th century.)

References

Macbride, J. E. A revision of the North American species of Amsinckia. Contr. Gray Herb. n.s. 49: 1–16. 1917.

Suksdorf, W. Untersuchungen in der Gattung Amsinckia, Werdenda 1:47–113. 1931.

Ray, Peter M. and H. F. Chisaki. Studies on Amsinckia, Amer. Journal Botany 44: 529–544. 1957.

1. Sepals 5, essentially distinct; corolla tube with 10 traces at the base; nutlets muricate or rugose .................... 1. *A. intermedia*

— Sepals 3–4, reduced in number, unequal in width; corolla tube with 20 traces at the base; nutlets smooth or tessellate .................... 2

2(1). Nutlets smooth .................... 2. *A. vernicosa*

— Nutlets tessellate .................... 3. *A. tessellata*

### 1. Amsinckia intermedia Fisch & Meyer

*Amsinckia intermedia* Fisch. & Mey. Ind. Sem. Hort. Petrop. 2: 26. 1836. (Near Bodega Bay, California)

*A. echinata* A. Gray, Proc. Amer. Acad. Arts 10: 54. 1876. (*J. G. Cooper*, sandy plains in the Mohave district of s.e. part of California, February 1861)

*A. parishii* Suksd. Werdenda 1: 70. 1931. (First specimen cited is S. *B. Parish 6043*, San Bernardino Valley, California, 10 April 1907)

*A. nana* Suksd. Ibid. 84: 1931. (*A. Eastwood 6016*, Hermit Creek, Grand Canyon of the Colorado River, Arizona, 10 April 1917)

*A. dimissa* Suksd. Ibid. 88: 1931. (*Norman C. Wilson*, Diamond Creek Canyon, Arizona, April 1893)

*A. ridida* Suksd. Ibid. 91: 1931. (First specimen cited is *F. Shreve 5134*, Tamamoe Hills, near Tucson, Arizona, 27 March 1917)

*A. arizonica* Suksd. Ibid. (First specimen cited is *A. Eastwood 6119*, Glendale, Arizona, 17 April 1917)

*A. microphylla* Suksd. Ibid. (*J. W. Tomey*, Tucson, Arizona, 3 April 1894)

*Stems* simple to erectly or widely branched 3–8(10) dm tall, sparsely spreading bristly; *leaves* at base of plant linear or linear-lanceolate 2–7(10) cm long, 1–5 mm broad, the upper leaves becoming lanceolate or lance-ovate, clasping at the base, the apex acute, thinly hirsute and pustulate on both surfaces; *inflorescence* open and spikelike, the spikes much elongating in fruit 5–15(25) cm long; *bracts* evident only at the base; *calyx* 5–7(10) mm long in fruit, the segments linear-lanceolate to linear, the tips attenuate, hirsute-hispid the hairs often rufous; *pedicels* 1–3 mm long, erect; *corolla* orange yellow, the tube 8–10 mm long, 10 nerved, the limb 3–6 mm broad; *style* 3–4 mm long, slender; *nutlets* ovate, 2.5–3 mm long, incurved, grayish, narrowly keeled on the back, sharply rugose, also muricate or papillate between the rugae. N = 15, 17, 19. (Ray & Chisaki 1957)

Dry to moderately moist places from the deserts to the grassy hills and meadows, a common roadside weed below 5,000 feet elevation. Washington to Baja California, Mexico, and eastward to Idaho, Utah, and Arizona. March to June.

*Amsinckia intermedia* is a highly variable species, especially in leaf shape and size, pubescence, and nutlet ornimentation. Suksdorf recognized over 100 species that fall within this taxon.

### 2. Amsinckia vernicosa H. & A.

*Amsinckia vernicosa* H. & A. Bot. Beechey Voy. 370. 1838. (*Douglas*, California, probably on his trip from Monterey to Santa Barbara)

*A. carnosa* M. E. Jones Contr. W. Bot. 8: 35. 1898. (*M. E. Jones*, Shepherds Canyon, alt. 4,600 feet, 30 April 1897)

*A. glauca* Suksd. Werdenda I: 113. 1931. (A. A. *Heller 7722*, Sunset, Kern County, California, 20 April 1905)

*Stems* simple or sparingly branched above, 2–6 dm tall, glabrous and glaucous or green, or occasionally with a few scattered bristles above; *leaves* nearly glabrous, 2–8 cm long, 2–10(14) mm broad, ovate-lanceolate to linear-lanceolate below, clasping, conspicuously pustulate ventrally less so below, the pustules sometimes producing a very short bristle, often ciliate-bristly on the margins; *inflorescence* open, terminating each branch, the spikes 3–12 cm long; *bracts* lacking or 1–2 at the base of the spike; *calyx* 8–11(15) mm long in fruit, the segments narrowly lanceolate, sometimes 2 or more partially united, hirsute-hispid with somewhat appressed and spreading pustulate bristles; *corolla* 10–12 mm long, limb 3–6 mm wide; *style* monomorphic; *nutlets* lance-ovate, 3–5 mm long, gray, smooth and shiny, the angles sharp and carinate, scar very narrow. N = 7.

Dry plains and hillsides, near sea level to moderate elevations in the mountains. Monterey and Fresno Counties, California, south to Kern County and east to the central Mohave Desert. March to May.

3. **Amsinckia tessellata** A. Gray

*Amsinckia tessellata* A. Gray, Proc. Amer. Acad. Arts 10: 54. 1874. (*W. H. Brewer 1119*, near Mount Diablo, Contra Costa County, California, 1862)

*A. tessellata* var. *macrosepala* M. E. Jones, Contr. W. Bot. 12: 58. 1908. *A. macrosepala* Suksd. Werdenda 1: 108. 1931. (Three specimens cited, no type given)

*A. macra* Suksd. Werdenda 1: 108. 1931. (*A. Eastwood 8025*, Sacaton, Arizona, 19 March 1919)

*Stems* branched just above the base and throughout, stout 3–6 dm tall, hispid, the bristles spreading, pustulate at base; *leaves* linear-lanceolate to ovate-lanceolate, 2–7 cm long, 4–15 mm broad, sessile, moderately hispid-pustulate on both surfaces; *inflorescence* spikelike, terminating each branch, the spikes 5–12(17) cm long; *bracts* lacking; *calyx* 9–13 mm long in fruit, the segments linear-lanceolate to oblong, 3 or 4 by fusion of 1 or 2 of the segments and then appearing notched at the apex, hispid, the back rufous, the margins white-ciliate; *corolla* orange, the tube 6–10 mm long, the limb 2.5–5 mm broad; *style* monomorphic; *nutlets* ovoid, 3–3.5 mm long, densely tessellate, carinate and often transversely rugose. N = 12.

Dry, mostly desert regions in sandy to rocky soils, on hillsides, bajadas, and mesas. Eastern Washington, southeast of the Cascades and Sierra Nevada, to southern California, Nevada, western Utah, Arizona, and southern New Mexico. March to June.

## 13. CRYPTANTHA Lehm.

### Catseye

Annual, biennial, or perennial, herbaceous or fruticulose plants; *stems* erect or ascending, usually with coarse stiff pubescence; *leaves* opposite at base, or alternate throughout, firm, veinless; *flowers* white or rarely yellow; *inflorescence* spikelike or racemose, bracted or bractless; *calyx* divided to the base, the lobes erect or connivent, linear or oblong, when mature investing the nutlets and falling away entire, or the calyx persistent and the nutlets falling away separately; *corolla* with a short to somewhat elongate cylindrical tube with or without scales at the base of tube, the fornices usually conspicuous; *style* slender, short or long, included; *stigma* capitate; *nutlets* 1–4, erect, ovate to triangular, roughened or smooth, winged, margined or marginless, affixed laterally through a median ventral and commonly basal forked groove; *gynobase* usually columnar, subulate, or pyramidal.

An exclusively American genus of about 100 species of western North and South America. (From the Greek, *cryptos*, hidden, and *anthos*, flower, because of the minute corolla in some species.)

### References

Johnston, I. M. The North American Species of *Cryptantha*. Contr. Gray Herb. 74: 1–114. 1925.

Payson, E. B. A Monograph of the Section Oreocarya of *Cryptantha*. Ann. Mo. Bot. Gard. 14: 211–358. 1927.

Higgins, L. C. A Revision of *Cryptantha* Subgenus Oreocarya Brigham Young Univ. Sci. Bull., Biol. Ser. 13(4):1–63. 1971.

1. Plants annual, with slender stems (of longer duration in *C. racemosa*) .......... 2
— Plants biennial or perennial .......... 34
2(1). Calyx circumscissle at maturity; low diffuse plant; inflorescence compact, each flower in axil of leafy bract .......... 1. *C. circumscissa*
— Calyx not circumscissle .......... 3

3(2). Gynobase subulate, protruding beyond the nutlets, bearing a sessile stigma on its tip; root and base of plant with a purple dye; each flower in the axil of a leafy bract .......... 2. *C. micrantha*

— Gynobase shorter than the nutlets; style developed; root or herbage usually with very little or no dye; flowers all or in part bractless (except *C. maritima*) .......... 4

4(3). Nutlets roughed or (in *C. maritima*) at least one of them so .......... 5

— Nutlets smooth and shining, not roughened .......... 31

5(4). Margins of nutlets decidedly winged or knifelike .......... 6

— Margins of the nutlets rounded or obtuse .......... 14

6(5). Pedicels usually evident, slender, 1–4 mm long; lateral angles of nutlets distinctly winged .......... 7

— Pedicels obscure or none, less than 1 mm long .......... 8

7(6). Nutlets homomorphous, broadly winged .......... 3. *C. holoptera*

— Nutlets heteromorphic, narrowly winged .......... 4. *C. racemosa*

8(6). Lateral margins of the nutlets usually distinctly winged; nutlets 4; calyx symmetrical .......... 9

— Lateral margins of the nutlets knifelike or acute .......... 10

9(8) Corolla conspicuous, 4–7 mm broad; nutlets homomorphic .......... 5. *C. oxygona*

— Corolla inconspicuous, ca. 1 mm broad; nutlets heteromorphic, the odd one often wingless .......... 6. *C. pterocarya*

10(8). Nutlets 1 or 2, odd nutlet axial .......... 7. *C. utahensis*

— Nutlets 4; odd nutlet abaxial .......... 11

11(10). Nutlets homomorphous; obscurely roughened .......... 12

— Nutlets heteromorphous, plainly muricate .......... 13

12(11). Nutlets lucid, somewhat bent, margin thickish .......... 8. *C. pusilla*

— Nutlets dullish, straight, margin thin, the back high, convex .......... 9. *C. costata*

13(12). Nutlets 1.3–1.7 mm long, the margins of the lateral angles knifelike; calyx 2.5–3.5 mm long, in fruit; corolla 1 mm broad .......... 10. *C. inaequata*

— Nutlets ca. 1 mm long, the margins of the lateral angles merely sharp; calyx ca. 3 mm long in fruit; corolla 1–2.5 mm broad .......... 11. *C. angustifolia*

14(5). Nutlets decidedly heteromorphous .......... 15

— Nutlets homomorphic .......... 20

15(14). Mature calyx strongly appressed to the flattened rachis, decidedly gibbous on the axil side, persistent .......... 12. *C. dumetorum*

— Mature calyx somewhat spreading, not at all gibbous .......... 16

16(15). Odd nutlet abaxial, surpassed by style .......... 17

— Odd nutlet axial; style surpassed or occasionally reaching to the nutlet tips .......... 18

17(16). Nutlets 1.3–1.7 mm long; calyx 2–3 mm long .......... 10. *C. inaequata*

— Nutlets ca. 1 mm long, calyx 3–4 mm long .......... 11. *C. angustifolia*

18(17). Odd nutlet smooth and shiny .......... 13. *C. maritima*

— Odd nutlet tuberculate or pappilate .......... 19

19(18). Spikes bracteate .......... 14. *C. minima*

— Spikes naked .......... 15. *C. crassisepala*

20(19). Style surpassing the nutlets .......... 21
— Style definitely surpassed by or about reaching to the tips of the nutlets .......... 25

21(20). Spikes bracted throughout .......... 22
— Spikes bractless or only sparingly so .......... 23

22(21). Plant spring flowering; stems dichotomously branched from the base outward; plant usually low 5–15 cm high, and spreading .......... 16. *C. mexicana*
— Plant summer flowering; main stems straight and erect, forming a central axis producing dichotomously branching laterals; plants usually taller, 15–40 cm high .......... 17. *C. albida*

23(21). Nutlets bent, lucid, gynobase narrowly pyramidal .......... 8. *C. pusilla*
— Nutlets straight, usually dull, gynobase subulate .......... 24

24(23). Nutlets triangular ovate, with a suggestion of a median dorsal ridge; plant dull dark green .......... 18. *C. muricata*
— Nutlets lanceolate or lance-ovate; plants canescent .......... 19. *C. intermedia*

25(24). Corolla conspicuous 2–5 mm broad .......... 26
— Corolla inconspicuous 0.5–22 mm broad .......... 27

26(25). Nutlets only 1 or 2 in a normal fruit; style not more than half as long as nutlet . .......... 20. *C. decipiens*
— Nutlets normally 4; style often more than half as long as nutlets .......... 19. *C. intermedia*

27(25). Nutlets usually solitary .......... 28
— Nutlets usually 4 .......... 29

28(27). Mature calyx and nutlet conspicuously recurved or deflexed .......... 21. *C. recurvata*
— Mature calyx and nutlets straight .......... 20. *C. decipiens*

29(27). Nutlets ovate or triangular ovate .......... 22. *C. echinella*
— Nutlets lanceolate .......... 30

30(29). Stems spreading hirsute .......... 23. *C. barbigera*
— Stems strigose .......... 24. *C. nevadensis*

31(4). Spikes bracteate, stems reddish .......... 13. *C. maritima*
— Spikes naked, stems greenish .......... 32

32(31). Style reaching one-fourth–three-fourths height of nutlets; calyx densely hispid-villous .......... 25. *C. gracilis*
— Style almost reaching the nutlet tips or surpassing them .......... 33

33(32). Margins of nutlets acute at least above the middle; Californian .......... 26. *C. mohavensis*
— Margin of nutlets rounded or obtuse; plants with a definite central axis; not californian .......... 27. *C. fendleri*

34(1). Corolla tube elongate, distinctly surpassing the calyx; flowers usually heterostyled .......... 35
— Corolla tube short, scarcely if at all surpassing the calyx; flowers not heterostyled .......... 44

35(34). Nutlets smooth and shining .......... 36
— Nutlets more or less roughened or wrinkled at least on the dorsal surface .......... 38

36(35). Corolla yellow .......... 37
— Corolla white .......... 30. *C. capitata*

37(36). Inflorescence an elongate, cylindrical thyrse; nutlets lanceolate, with acute margins, usually only one developing .......... 28. *C. flava*
— Inflorescence consisting of a large terminal cluster with one or more remote, at maturity frequently stalked, much smaller lateral clusters; nutlets broadly ovate, with winged margins, all four usually maturing .......... 29. *C. confertiflora*

38(35). Nutlets muricate or verrucose .......... 31. *C. fulvocanescens*
— Nutlets rugose or tuberculate .......... 39

39(38). Ventral or inner surface of the nutlets smooth or nearly so .......... 40
— Ventral surface of the nutlets distinctly roughened .......... 41

40(39). Corolla tube 7–10 mm long; calyx lobes 5–7 mm long in anthesis; plants not heterostyled; nutlets conspicuously tuberculate and short rugose .......... 32. *C. oblata*
— Corolla tube 12–14 mm long; calyx lobes 7–9 mm long in anthesis; plants strongly heterostyled; nutlets finely tuberculate or rugose .......... 33. *C. paysonii*

41(39). Inflorescence 0.1–0.4 dm long; corolla tube 10–12 mm long; margins of nutlets not in contact; plants less than 1.2 dm tall .......... 34. *C. paradoxa*
— Inflorescence 0.5–3 dm long; corolla tube 5–10 mm long; margins of nutlets in contact or nearly so; plants usually over 1.2 dm tall .......... 42

42(41). Scar of nutlets surrounded by an elevated margin but tightly closed; style 1–2 mm long; calyx 3.5–4 mm long in anthesis .......... 35. *C. bakeri*
— Scar of nutlets conspicuously open; style 3–8 mm long; calyx 4.5–7 mm long in anthesis .......... 43

43(42). Corolla tube 7–10 mm long; scar of nutlets conspicuously open and surrounded by a definite elevated margin .......... 36. *C. flavoculata*
— Corolla tube 5–7 mm long; scar of nutlets slightly open and with only an inconspicuous elevated margin if any .......... 37. *C. tenuis*

44(34). Nutlets smooth on their dorsal surface .......... 45
— Nutlets more or less roughened on the dorsal surface .......... 47

45(44). Plants strong perennials; crests at base of corolla tube conspicuous; calyx not noticable accrescent, widespread species .......... 38. *C. jamesii*
— Plants biennial or weak perennials; crests at base of corolla tube lacking; calyx noticable accrescent .......... 46

46(45). Inflorescence capitate or nearly so; calyx segments in fruit 5–7 mm long, a narrow endemic of Coconino Co., Arizona .......... 39. *C. atwoodii*
— Inflorescence broad topped due to the elongation of the cymules in age; calyx segments in fruit 7–10 mm long; SE New Mexico south into Texas and Mexico . .......... 40. *C. palmeri*

47(44). Ventral surface of nutlets smooth or nearly so .......... 48
— Ventral surface of nutlets rugose or variously roughened .......... 49

48(47). Nutlets bordered by a conspicuous wing; robust plants 5–10 dm tall, with long ebractate spikes; Arizona .......... 41. *C. setosissima*
— Nutlets never conspicuously winged; plants 2–4 dm tall; inflorescence very broad and bracteate; NE New Mexico .......... 42. *C. thyrsiflora*

49(47). Scar somewhat constricted below the middle of the open portion, NE Arizona . .......... 43. *C. osterhoutii*

– Scar triangular and not constricted below the middle or (closed in *C. bakeri*) .... .......... 50

50(49). Cymules elongating and so the inflorescence broad; biennial or short-lived perennials; nutlets usually with an evident dorsal ridge .......... 51

– Cymules shorter and the inflorescence narrow; long-lived perennials; nutlets with only a slight dorsal ridge if any .......... 53

51(50). Surface of the leaves with inconspicuous appressed bristles; inflorescence open, with only a few elongate cymules, 7–14 cm long terminating the stem; endemic to near Las Vegas, Nevada; known only from the type and may not exist any longer due to urbanization in the area .......... 44. *C. insolita*

– Surface of the leaves conspicuously setose-hispid with spreading bristles; inflorescence open, at least at maturity .......... 52

52(51). Calyx lobes 7–12 mm long in fruit; nutlets 3–4.5 mm long, prominately carinate on the dorsal side .......... 45. *C. virginensis*

– Calyx lobes 5–7 mm long in fruit; nutlets 2.5–3 mm long, with only an indistinct central ridge toward the apex .......... 46. *C. hoffmannii*

53(50). Nutlets indefinitely tuberculate and rugose to nearly smooth; W Nevada and E California .......... 47. *C. tumulosa*

– Nutlets definitely tuberculate, rugose or muricate .......... 54

54(53). Scar of nutlets open .......... 55

– Scar of nutlets closed .......... 35. *C. bakeri*

55(54). Ventral surface of nutlets deeply rugose and tuberculate, the dorsal less so ........ .......... 48. *C. abata*

– Ventral surface of nutlets muricate or verrucose, the dorsal also or with some of the murications connected to form short irregular ridges .......... 49. *C. humilis*

1. **Cryptantha circumcissa** (H. & A.) I. M. Johnston

*Lithospermum circumscissum* H. & A. Bot. Beechey Voy. 370. 1840. *Piptocalyx circumscissus* Torr. in S. Wats. Bot. King Exp. 240. 1871. *Eritrichium circumscissum* A. Gray, Proc. Amer. Acad. Arts 10: 58. 1874. *Krynitzkia circumscissa* A. Gray, Proc. Amer. Acad. Arts 20: 275. 1885. *Wheelerella circumscissa* Grant, Bull. S. Calif. Acad. Sci. 5: 28. 1906. *Greeneocharis circumscissa* Rydb. Bull. Torrey Club 36: 677. 1901. *Cryptantha circumscissa* I. M. Johnst. Contr. Gray Herb. 68: 55. 1923. (*Tolmie*, Snake Ft. Snake County, Idaho)

Small annual herbs; *stems* erect or bushy branched, forming round clumps 0.2–1 dm tall, strigose to very hirsute; *leaves* oblanceolate to nearly linear, 0.4–1.5 cm long, 1–2 mm broad, obtuse, strigose or hirsute, pustulate with small inconspicuous pustules, the petioles somewhat siliceous; *inflorescence* short, congested, the racemes obscure; *bracts* evident, appearing as if a continuation of the foliage leaves; *calyx* 2.5–4 mm long in fruit, oblong-ovate, connate to near the middle, the lobes falling away by a circumscission near the sinuses, hirsute, the tube ciliceous, persistent; *pedicels* about 0.5 mm long; *corolla* minute, white, inconspicuous, 1–2(3) mm broad; *style* just exceeded by the nutlets or equalling them; *gynobase* about ⅔ height of nutlet; *nutlets* 4, homomorphous, or with the abaxial one slightly larger, triangular-ovate or oblong-lanceolate, 1.2–1.7 mm long, margins acute, the surfaces smooth or inconspicuously muriculate, scar closed and forked below.

Dry, open, usually sandy slopes and plains, widely distributed in many plant communities, however in our area found mostly in the *Larrea* and *Juniperus* communities. Central Washington to Baja California, mostly east of the Cascade and Sierra Nevada ranges to southern Idaho, Utah, and Arizona; also Chile and Argentina. March to July.

2. **Cryptantha micrantha** (Torr.) I. M. Johnston

*Eritrichium micranthum* Torr. Bot. Mex. Bound. 141. 1859. *Krynitzkia micrantha* A. Gray, Proc. Amer. Acad. Arts 20: 275. 1885. *Eremocarya micrantha*

E. L. Greene, Pittonia 1: 59. 1887. *C. micrantha* I. M. Johnst. Contr. Gray Herb 68: 56. 1923. (*Thurber*, sand hills, Frontera, Texas, and in other places along the Rio Grande, March-April)

*Eremocarya muricata* Rydb. Bull. Torrey Club 36: 677. 1909. (*Parry 164*, Valley of the Virgin near St. Gewrge)

*Eritrichium micranthum* var. *lepidum* A. Gray. Syn. Fl. N. Amer. 2 pt. 1. 193. 1886. *Krynitzkia micrantha* var. *lepida* A. Gray, Proc. Amer. Acad. Arts 20: 275. 1885. *Eremocarya lepida* E. L. Greene, Pittonia 1: 59. 1887. *Eremocarya micrantha* var. *lepida* Macbr. Proc. Amer. Acad. Arts 51: 545. 1916. *Cryptantha micrantha* var. *lepida* I. M. Johnst. Contr. Gray Herb. 68: 57. 1923. (*Cleveland*, San Diego, California, 1876) = var. *lepida*

Slender annual herbs; *stems* dichotomously branched throughout, 0.5–1.5 dm tall, root and lower part of the stem dye stained, strigose; *leaves* linear to oblong-oblanceolate, 0.3–0.7 cm long, 0.8–1.4 mm wide, strigose to villous-hirsute, pustulate on the dorsal side; *inflorescence* short, dense, 1–4 cm long, the spikes unilateral solitary or geminate, numerous; *bracts* conspicuous, subtending each flower; *calyx* 1.8–2.5 mm long in fruit, ovate-oblong, slightly asymmetrical, conspicuously biseriate, the segments oblong-lanceolate, hirsute; *pedicels* 0.5–0.8 mm long; *corolla* inconspicuous to evident, 0.5–2.5(3.5) mm broad; *style* short, the stigma sessile; *gynobase* subulate, much longer than the nutlets; *nutlets* 4, homomorphous to slightly heteromorphous, the abaxial one the most persistent and slightly larger, lanceolate with apex attenuate, 1–1.3 mm long, margins rounded, plumbeous or brown, smooth or tuberculate, scar extending entire length of nutlet, narrow, only slightly broadened at the base.

Dry, open, sandy slopes and plains. Nevada and Utah, south to Baja California and Arizona, eastward to southern New Mexico and Transpecos Texas; also northern Mexico. March to June.

The species is easily recognized because of its dense bracteate spikes, dye-stained root, and the long, protruding gynobase.

3. **Cryptantha holoptera** (A. Gray) MacBride

*Eritrichium holopterum* A. Gray, Proc. Amer. Acad. Arts 12: 81. 1876. *Krynitzkia holoptera* A. Gray, Ibid. 20: 276. 1885. *Oreocarya holoptera* E. L. Greene, Pittonia 1: 58. 1887. *Cryptantha holoptera* Macbride, Contr. Gray Herb. 48: 44. 1916. (*E. Palmer*, Ehrenber, Arizona, 1876)

Coarse annual herbs; *stems* erect, somewhat woody toward the base, 1–6 dm tall, the branches ascending, rather numerous, hirsute also somewhat strigose; *leaves* oblanceolate to linear-lanceolate, 3–6 cm long, 3–8(12) mm wide, hirsute, conspicuously pustulate on the dorsal side, less so above; *inflorescence* racemose, the racemes usually geminate, 0.4–0.7(1) dm long; *bracts* inconspicuous or evident on a few racemes; *calyx* 2.5–3.5 mm long in fruit, oblong-ovate, the segments lanceolate, connivent, midrib thickened and hirsute; *pedicels* ascending or recurved, 0.7–1.5 mm long; *corolla* white, minute; *style* evidently surpassing the nutlets; *gynobase* slender, nearly equalling the nutlets; *nutlets* 4, homomorphous, ovate to slightly oblong-ovate, 1.5–2.5 mm long, margins narrowly to broadly winged, the surface of the nutlets dark with lighter tuberculations, scar subulate, closed above, clearly open below.

Dry, gravelly, or rocky slopes and ridges mostly in the *Larrea* community. Inyo County, California, south to southern Imperial County, California, and eastward to Mohave and Yuma counties, Arizona, not common. February to April.

4. **Cryptantha racemosa** (S. Wats.) E. L. Greene

*Eritrichium racemosum* S. Wats. in A. Gray, Proc. Amer. Acad. Arts 17: 226. 1882. *Krynitzkia racemosa* E. L. Greene, Bull. Calif. Acad. Sci. 1: 208. 1855. *C. racemosa* E. L. Greene, Pittonia 1: 115. 1887. *Johnstonella racemosa* Brand, Feddes Repert. Spec. Nov. Regni Veg. 21: 249. 1925. (*S. B. & W. F. Parish 775*, canyon near Mesquite Station, San Bernardino County, California, March 1881)

*C. suffruticosa* Piper, Proc. Biol. Soc. Wash. 32: 42. 1919. (*Orcutt* 2070, Camp Muchacho, Colorado Desert)

*C. racemosa* var. *lignosa* I. M. Johnst. Univ. Calif. Publ. Bot. 7: 445. 1922. *J. racemosa* var. *lignosa* Brand, Feddes Repert. Spec. Nov. Regni Veg. 21: 249. 1925. (*Hall & Chandler 7034*, Panamint Canyon, Panamint Mountains, California)

Long-lived somewhat suffruticose annual; *stems* simple, with many ascending branches or diffusely branched from near the base, 1–10 dm tall, younger parts green, hirsute and also strigose, older parts brown, woody, with exfoliating epidermis; *leaves* oblanceolate, acute, hirsute, conspicuously pustulate, 1.5–4(6) cm long, 2.5–4(12) mm broad; *inflorescence* paniculate, the racemes branched and loosely flowered, 0.3–1.5 dm long; *bracts* irregular and inconspicuous; *calyx* 2–4 mm long in fruit, oblong-ovate, tardily deciduous, the segments linear-lanceolate, strigose and hirsute along the thickened midrib; *pedicels* 1–4 mm long, slender, frequently recurved; *corolla* very inconspicuous, about 1 mm broad; *style* much surpassing the nutlets; *gynobase* subulate, nearly equalling the consimilar nutlets; *nutlets* 4, heteromorphous, ovate, the acute tips slightly out-curved, odd nutlet next the abaxial calyx-lobe, 1–2 mm long, subpersistent, muricate or tuberculate or both, consimilar nutlets 0.8–1.5 mm long, the margins narrowly winged, dark with pale tuberculations, scar open or closed above, but opening out into a triangular areola below.

Dry, sandy slopes or rocky ridges mostly below 4,500 feet. Inyo County, California, south to northeastern Baja California and eastward to southern Nevada, southwestern Utah, and Mohave and Yuma counties, Arizona, not common. March to June.

*Cryptantha racemosa* is the only annual with stems that become somewhat woody or subfruticose near the base.

5. **Cryptantha oxygona** (A. Gray) Greene

*Eritrichium oxygonum* A. Gray, Proc. Amer. Acad. Arts 19: 89. 1883. *Krynitzkia oxygona* A. Gray, Proc. Amer. Acad. Arts 20: 227. 1885. *C. oxygona* E. L. Greene, Pittonia 1: 120. 1887. (*C. G. Pringle*, hills bordering the Mohave Desert, California, 1882)

Erect annual herbs; *stems* mostly solitary, 1–4 dm tall, with several well-developed ascending branches from near the base, strigose also villous-hispid; *leaves* linear or linear-lanceolate, 1–4(6) cm long, 1–2(3) mm broad, strigose or short-hispid, obtusish, pustulate with small numerous inconspicuous pustules; *inflorescence* dense, the spikes geminate or ternate, 1–3(6) cm long; *bracts* lacking; *calyx* 2.5–4 mm long in fruit, ovate to oblong-ovate, obscurely biserial, the segments lanceolate, with somewhat thickened sparsely hirsute midribs, the margins silky strigose, somewhat connivent; *pedicels* short 0.5 mm long; *corolla* conspicuous, the limb 4–7 mm broad; *style* evidently surpassing the nutlets; *gynobase* about two-thirds as long as nutlets, nearly subulate; *nutlets* 4, homomorphous, oblong-ovate, 2–2.5(3) mm long, margins narrowly winged or knifelike, dorsal side of nutlet low convex, muricate or tuberculate, scar closed or open above, open below with a broadly forked triangular areola.

Dry slopes and benches below 5,000 feet. California in the inner southern Coastal Ranges from western Merced and Fresno counties to Kern County, western Mohave Desert to Santa Rosa Mountains, Riverside County, eastward just into western Nevada. March to May.

A species closely related to *C. pterocarya* but having much larger corollas, and ranging more westward, just entering our flora along the western boundary in Kern County.

6. **Cryptantha pterocarya** (Torr.) E. L. Greene

*Eritrichium pterocaryum* Torr. Bot. Mex. Bound. 142. 1859. *Krynitzkia pterocarya* A. Gray, Proc. Amer. Acad. Arts 20: 276. 1885. *C. pterocarya* E. L. Greene, Pittonia 1: 120. 1887. (*Pickering & Brackenridge 1047*, Walla Walla, Washington; lectotype by I. M. Johnston)

*Eritrichium pterocaryum* var. *pectinatum* A. Gray, Proc. Amer. Acad. Arts 10: 61. 1874. *Krynitzkia pterocarya* var. *pectinata* A. Gray, Proc. Amer. Acad. Arts 20: 276. 1885. (*C. C. Parry 168, 169*, in the Virgin River Valley near St. George, Utah) = var. *pterocarya*.

*Krynitzkia cycloptera* E. L. Greene, Bull. Calif. Acad. Sci. 1: 207. 1884. *C. cycloptera* E. L. Greene, Pittonia 1: 120. 1887. *C. pterocarya* var. *cycloptera* Macbr. Contr. Gray Herb. 48: 44. 1916. (*C. G. Pringle*, hills near Tucson, Arizona, 1884) = var. *cycloptera*

Erect annual herb; *stems* 1–4 dm tall, ascendingly branched from the base and throughout, strigose or very short hirsute; *leaves* lanceolate to linear, 1–2.5(4) cm long, 1–3(5) mm broad, obtuse, strigose or hispid, dorsal surface conspicuously pustulate, ventral surface finely pustulate or the pustules nearly lacking; *inflorescence* open, the spikes geminate or rarely solitary or ternate, 2–6(12) cm long; *bracts* inconspicuous or lacking; *calyx* in fruit (2)3–5 mm long, very accrescent, broadly ovate, the segments ovate to ovate-lanceolate, the midrib slightly thickened and sparsely hirsute, the margins tawny strigose or hirsute; *pedicels* 0.5–1 mm long; *corolla* inconspicuous, 0.5–1(2) mm broad; *style* surpassing the body of nutlet but occasionally surpassed by the broad wing margin of nutlet; *gynobase* slender, about two-thirds height of nutlet; *nutlets* 4, homomorphous and all winged or heteromorphous and the axial one wingless, the body oblong-lanceolate or lanceolate, 2–2.5(3) mm long, margin of nutlet broad and winglike or narrow, entire but usually crenate, entending completely around the nutlet, surface muricate, scar open or closed above, at the base opening into a dilated areola.

Dry sandy to gravelly washes and bajadas, below 6,000 feet. East of the Cascades and Sierra Nevada from southern Washington to northern Baja California, eastward to southern Idaho, Utah, Arizona, and northern Sonora, Mexico. March to June.

*Cryptantha pterocarya* can be separated into two rather weak varieties on the basis of the nutlets as follows:

1. Nutlets heteromorphic, axial one wingless .......................................... var. *pterocarya*
— Nutlets homomorphic, all winged ............................... var. *cycloptera* (Greene) Macbr.

Variety *pterocarya* tends to be more southerly ranging than variety *cycloptera*; also there are very few intermediates between the two varieties.

7. **Cryptantha utahensis** (A. Gray) E. L. Greenell

*Krynitzkia utahensis* A. Gray, Synop. Fl. N. Amer. 2: pt. 1. suppl. 427. 1886. *C. utahensis* E. L. Greene, Pittonia 1: 120. 1887. *Eritrichium holopterum* var. *submolle* A. Gray, Proc. Amer. Acad. Arts 13: 374. 1878. *Cryptantha submollis* Coville, Contr. U. S. Natl. Herb. 4: 166. 1893. (*E. C. Palmer* 352, St. George, Utah)

Erect ascendingly branched herb; *stem* solitary at base branched just above the base and throughout, 1–3(4) dm tall, strigose or appressed short hirsute; *leaves* few, scattered, reduced above, linear to linear-oblanceolate 1–5(7) cm long, 1–4 mm broad, obtuse, short hirsute, conspicuously pustulate especially on the dorsal surface, less so above; *inflorescence* open, the spikes geminate or solitary, dense, 0.8–2.5(5) cm long; *calyx* 2–3(4) mm long in fruit, ovate to oblong, the base oblique-conic, spreading or recurving, the segments lanceolate, strongly connivent, the brownish thickened midrib occasionally bearing spreading or recurved bristles, the margins densely silky villous-hirsute; *pedicels* obscure; *corolla* conspicuous 2–4(5) mm broad; *style* just slightly shorter than nutlets; *gynobase* subulate, differing only slightly from the style; *nutlets* 1 or rarely 2, lanceolate, 1.7–2.5 mm long, margins acute or with a narrow knifelike wing, the surface pale, muricate, papillate, or occasionally spinulose, the back low convex or flat, scar open, linear and slightly dilated below into a small areola.

Dry, sandy or rocky washes and hillsides. Desert region of Inyo, San Bernardino, and Riverside counties, California, eastward through southern Nevada into southwestern Utah, and western Arizona in Mohave County. March to May.

8. **Cryptantha pusilla** (Torr. & Gray) E. L. Greene

*Eritrichium pusillum* Torr. & Gray, Pacif. R. R. Report 2: 171. 1856. *Krynitzkia pusilla* A. Gray, Proc. Amer. Acad. Arts 20: 174. 1885. *C. pusilla* E. L. Greene, Pittonia 1: 115. 1887. (*Pope*, Rio Pecos to Llano Estacado, March)

Low annual herbs; *stems* numerous, prostrate to ascending, very slender, 0.3–1.5 dm tall, canescent, strigose to villous-hirsute; *leaves* mostly basal, scattered above, linear to linear-spathulate, 1–3 cm long, 1–2 mm wide, hispidulous and pustulate on the dorsal surface, less so ventrally; *inflorescence* compact, the spikes solitary or geminate, 2–8 cm long, densely flowered; *bracts* lacking or the bracts few and minute; *calyx* 2–2.5 mm long in fruit, broadly ovate, early deciduous, the segments ovate-lanceolate or oblong-lanceolate, hirsute, the midrib only slightly thickened; *pedicels* obscure; *corolla* minute, shorter than the calyx, about 0.6 mm wide; *style* conspicuously surpassing the nutlets; *gynobase* narrowly pyramidal, about equalling the nutlets; *nutlets* 4, homomorphous, lucid, broadly ovate, bent, 0.8–1.2 mm long, margins acute or knifelike, surface light brown or tan with pale tuberculations, scar subulate and expanded at base into a triangular areola.

Dry, sandy or gravelly slopes and washes. Southern Arizona east through southern New Mexico into Trans Pecos Texas; ranging southward into Sonora, Chihuahua, and Durango, Mexico. March to May.

*Cryptantha pusilla* is a relatively rare plant which just enters our area along the southern boundary or the Mexican border.

9. **Cryptantha costata** Brandegee

*Cryptantha costata* Brandegee, Bot. Gaz. 27: 453. 1899. (*Brandegee*, Borregos Springs, California, 1895)

*C. seorsa* Macbride, Contr. Gray Herb. 48: 46. 1916. (*M. E. Jones 3841*, Needles, California)

Coarse low annual herbs; *stems* erect, few branched, 1–2 dm tall, densely villous-strigose and somewhat hirsute; *leaves* lanceolate to linear, 1–3 cm long, 2–4 mm wide, dorsal surface hispid, also pustulate, ventral surface villous-strigose and sparsely hispidulous the pustules few and inconspicuous; *inflorescence* open, the spikes rigid, solitary or geminate, 2–5 cm long; *bracts* remote, few; *calyx* in fruit 4–6 mm long, ovate-oblong, deciduous, the segments linear lanceolate, connivent with slightly spreading tips, midrib thickened, hirsute, margins strigose; *pedicels* obscure; *corolla* inconspicuous, the tube shorter than the calyx, the lobes ascending; *style* very similar to the gynobase, much surpassing the nutlets; *gynobase* subulate; *nutlets* 4, homomorphous, or slightly heteromorphous with the nutlet next the abaxial calyx-lobe the largest, triangular or oblong-ovate, 1.6–1.9(2) mm long, margins knifelike or narrowly winged, dorsal surface strongly convex, slightly rugulose or obscurely muriculate, ventral surface flat or slightly concave, scar shallow, closed above opening below into a triangular-subulate areola.

Dry sandy washes and bajadas. Inyo County to San Diego County, California, eastward just into Arizona in Yuma County. February to May.

An interesting plant because of its unusual nutlets which have a flat ventral face and a very high, convex dorsal surface.

10. **Cryptantha inaequata I. M. Johnston**

*C. inaequata* I. M. Johnst. Univ. Calif. Publ. Bot. 7: 444. 1922. *Johnstonella inaequata* Brand, Feddes Repert. Spec. Nov. Regni. Veg. 21: 250. 1925. (*Hall & Chandler 6925*, among rocks, Pleasant Canyon, Panamint Mountains, California, 600 meters altitude)

Erect annual herbs; *stems* ascendingly branched, coarse, 2–4 dm tall, hispid and strigose; *leaves* linear to linear-oblanceolate, 1.5–4 cm long, 1–3(4) mm broad, acute, hispid, pustulate on the dorsal surface; *inflorescence* open, the spikes solitary or geminate, 4–12 cm long; *bracts* few and scattered or lacking; *calyx* in fruit 2–3(4) mm long, ovate-oblong, the segments lanceolate midrib moderately thickened and hirsute, axial lobe the most thickened and hirsute; *pedicels* very short, less than 0.5 mm long; *corolla* small, 1–2(3) mm broad; *style* conspicuously surpassing the nutlets; *gynobase* narrowly subulate, equalling consimilar nutlets; *nutlets* 4, heteromorphous, triangular-ovate, margins acute or knifelike, surface brownish with pale tuberculations, odd nutlet about 1.7 mm long, more persistent and slightly lighter in color than the others, next the abaxial calyx-lobe, the consimilar nutlets 1.3–1.5 mm long, scar subulate, closed above, narrowly triangular below.

Dry, usually clay soils, on desert slopes and rocky ridges. Inyo and San Bernardino counties, California, eastward to southern Nevada, southwestern Utah, and western Arizona in Mohave County. March to May.

This species is relatively rare throughout its range, but in certain localities, as northeast of Henderson, Nevada, it becomes more common, especially when the moisture supply is sufficient. The species is nearly always on heavy gumbo clay soil.

11. **Cryptantha angustifolia** (Torr.) E. L. Greene

*Eritrichium angustifolium* Torr. Pacif. R. R. Reports 5: 363. 1857. *Krynitzkia angustifolia* A. Gray, Proc. Amer. Acad. Arts 20: 272. 1885. *C. angustifolia* E. L. Greene, Pittonia 1: 112. 1887. (*Thomas*, Fort Yuma, Arizona)

Diffuse annual herbs; *stems* much branched from near the base, ascending to nearly decumbent, 0.5–2(3) dm tall, hirsute to strigose-villous; *leaves* linear, 1.5–4 mm long, 1–2(4) mm wide, hispid or strigose, pustulate especially on the dorsal surface; *inflorescence* rather dense, the spikes geminate, 2.5–6(9) cm long, densely flowered; *bracts* lacking, *calyx* in fruit 2–4 mm long, ovate-oblong, ascending, strongly biseriate, the segments linear-lanceolate, midrib thickened and hirsute, the margins villous-hirsute and ciliate; *pedicels* obscure, less than 0.5 mm long, *corolla* inconspicuous to evident, 1–2.5 mm broad; *style* usually surpassing even the odd nutlet; *gynobase* columnar, equalling the consimilar nutlets; *nutlets* usually 4, heteromorphous, ovate-oblong, margins obtuse, acute, or narrowly winged, the surface brown with pale tuberculations or murications, odd nutlet next abaxial calyx-lobe, slightly larger than the consimilar nutlets which are about 1 mm long, scar very narrowly linear-lanceolate.

Dry, sandy or gravelly washes. Southeastern California from the Death Valley region to northeastern Baja California and eastward to southwestern Utah, western Texas, and Sonora, Mexico. March to June.

12. **Cryptantha dumetorum** E. L. Greene
*Krynitzkia dumetorum* Greene, Pittonia 1: 112. 1887. (*Curran*, half climbing among bushes at Tehachapi Pass, California 1884)

Sprawling annual herb; *stems* erect, or in age, elongate and scrambling or supported by various shrubs, 1–4(5) dm tall, closely strigose; *leaves* lanceolate, 1–3(4) cm long, 2–4(8) mm wide, thickish, sparsely appressed hispidulous, conspicuously pustulate on the dorsal surface, less so above; *inflorescence* open, the spikes solitary or geminate, loosely flowered, 5–10 cm long; *bracts* mostly lacking or occasionally with 1 or 2 near the base; *calyx* in fruit 2–3 mm long, closely appressed to the flattened rhachis, conspicuously asymmetrical, persistent, gibbous at the base on the axial side, the 3 abaxial lobes lanceolate, with thickened hispid midribs, the 2 axial lobes partly united, strigose and deflexed hispid; *pedicels* lacking; *corolla* minute, about 1 mm broad; *style* subequal to nutlets or slightly shorter than the nutlets; *gynobase* subulate, narrow; *nutlets* 4, heteromorphous, ovate-lanceolate, to lanceolate, muricate, odd nutlet axial, persistent, 2–3 mm long, the base enlarged and distorting the calyx, scar open and broad, consimilar nutlets 1.5–2 mm long, deciduous, scar closed or very narrow and linear.

Sandy bajadas and hillsides or occasionally in the wash bottoms. Central Mohave Desert of California eastward through southern Nevada into southwestern Utah. April to May.

The Utah collection of this species is from the west shore of Ivins Reservoir, a considerable extension of range from that previously known. The plant probably also occurs in Mohave County, Arizona, but has not been documented.

13. **Cryptantha maritima** E. L. Greene
*Krynitzkia maritima* E. L. Greene, Bull. Calif. Acad. Sci. 1: 204. Aug. 1885. *C. maritima* E. L. Greene, Pittonia 1: 117. 1887. (*E. L. Greene*, Guadalupe Island, California, 26 April 1885)
*Krynitzkia ramosissima* E. L. Greene, Bull. Calif. Acad. Sci. 1: 203. Aug. 1885. non *K. ramosissima* A. Gray 1885. (*Mrs. Curran*, Mohave Desert, California, 1884)
*C. maritima* var. *pilosa* I. M. Johnst. Univ. Calif. Publ. Bot. 7: 445. 1922. (*Palmer 551*, stony ridges, Los Angeles Bay, Lower California)

Erect annual herbs; *stems* reddish, ascendingly branched throughout, 1–3(4) dm tall, mostly strigose or occasionally hirsute; *leaves* linear to lanceolate, acutish, 1–3.5 cm long, 1–3.5 mm wide, sparsely hirsute, coarsely pustulate; *inflorescence* dense, the spikes solitary or geminate 1–7(12) cm long, congested, or glomerate especially when immature; *bracts* evident, and scattered throughout; *calyx* in fruit 1–3(3.5) mm long, ovate-oblong, ascending, deciduous at length, the segments linear-lanceolate, connivent, the midrib thickish and hirsute, the margins hirsute-villous to villous; *pedicels* obscure or lacking; *corolla* minute, 0.5–1 mm broad; *style* nearly equalling consimilar nutlet; *gynobase* subulate one-half–two-thirds length of nutlets; *nutlets* 1–4, heteromorphous, odd nutlet often the only one developing, abaxial, lanceolate, 1–2 mm long, margins rounded, surface smooth and shiny, brownish, scar closed or open at base into a small areola, consimilar nutlets similar, but tuberculate and grayish, early deciduous.

Dry washes and desert bajadas. Inyo County and throughout southeastern California to northern Baja California and east to southern Nevada, southwestern Utah, Arizona, and Sonora, Mexico. March to May.

The variety *pilosa* I. M. Johnston, is distinguished from the typical material by the densely white-villous calyx-segments. The range of *pilosa* is scattered within the range of the species.

14. **Cryptantha minima** Rydb.
*C. minima* Rydb. Vull. Torrey Club 28: 31. 1901. (*Rydberg* & *Vreeland 5697*, Cuchara River, above La Veta, Colorado, 2100 m)

Small annual herbs; *stems* erect or ascending-spreading, numerous, 0.5–1.5(2) dm tall, finely strigose and coarsely hirsute; *leaves* oblanceolate, 1–3(4) cm long, 1.5–4 mm broad, obtuse, hirsute or hispid in age, moderately pustulate; *inflorescence* dense, the spikes solitary or occasionally geminate 2–9(15) cm long; *bracts* evident throughout; *calyx* in fruit 4–7(9) mm long, oblong-ovate, spreading, asymmetrical, the segments lance-linear, connivent, midrib conspicuously thickened and bony, hispid, margins sparsely hirsute or appressed hispid; *pedicels* short, 0.5–1.5 mm long; *corolla* small, 1–1.5 mm broad; *style* surpassed by odd nutlet, equalling or surpassing consimilar ones; *gynobase* oblong about 0.7 mm long; *nutlets* 4, hetermorphous, odd nutlet ovate 2–3 mm long, margins angled, the surface brownish, finely muriculate or granulate, persistent, next abaxial calyx-lobe, consimilar nutlets 1.2–1.5 mm long, thick, tuberculate, scar broadly open especially at the base, not forked.

Widely distributed on great variety of soils. Principally on the plains east of the Continental Divide, from Saskatchewan, Canada, south to northern New Mexico and Texas. April to July.

This plant is closely related to *C. crassisepala* (Torr. & Gray) Greene, a more southern and westwardly growing species. The bracted inflorescences serve best to distinguish it from its southern relative.

15. **Cryptantha crassisepala** (Torr. & Gray) E. L. Greene

*Eritrichium crassisepalum* Torr. & Gray, Pacif. R. R. Reports 2: 171. 1857. *Krynitzkia crassisepala* A. Gray, Proc. Amer. Acad. Arts 20: 268. 1885. (*Pope*, vicinity of Permanent Camp on Rio Pecos, 6–7 April 1856)

*C. dicarpa* A. Nelson, Proc. Biol. Soc. Wash. 16: 30. 1903. (*T. D. A. Cockerell 30*, Mesilla Park, New Mexico) = var. *crassisepala*

*C. crassispela* var. *elachantha* I. M. Johnst. Wrightia 2: 20. 1959. (*R. McVaugh 8040*, north end of Quitman Mountains, 8 miles west of Sierra Blanca, Hudspeth County, Texas) = var. elachantha

Erect or spreading annual herbs; *stems* many, ascendingly branched, 0.5–1.5(2.5) dm tall, hirsute to hispid; *leaves* oblanceolate, 1–3(6) cm long, 2–4(6) mm wide, rounded or obtuse, hirsute, pustulate, the upper scarcely reduced; *inflorescence* moderately dense, the spikes solitary or geminate 3–10(15) cm long; *bracts* lacking or 1 to 2 subtending the lowermost flowers; *calyx* in fruit 5–7(10) mm long, oblong-ovate, slightly asymmetrical, the segments lance-linear, connivent above, midrib very hard and thickened, hispid-hirsute; *pedicels* about 0.5–1 mm long; *corolla* inconspicuous to 5 mm in diameter; *style* surpassed by odd nutlet, equalling or slightly longer than consimilar ones; *gynobase* narrowly oblong; *nutlets* 4, or occasionally less by abortion, heteromorphous, odd nutlet persistent, next abaxial calyx-lobe, ovate, acute, 2–2.5(3) mm long, the surface granulate or spinular-muricate, brownish, consimilar nutlets early deciduous, ovate-oblong, 1.2–1.5(2) mm long, tuberculate, scar large, open, occupying most of ventral surface.

Usually dry sandy soils on ridges and in washes. Southern Utah and Arizona, eastward to southwestern Colorado, New Mexico, western Texas, and northern Mexico. March to July.

16. **Cryptantha mexicana** (Brandeg.) I. M. Johnston

*Krynitzkia mexicana* Brandeg. Zoe 5: 182. 1905. *C. mexicana* I. M. Johnst. Wrightia 2: 161. 1961. (*Purpus 8301*, near Viesca, southwestern Coahuila, Mexico, 1903)

Dense, low, rounded herbs; *stems* numerous, erect, spreading or ascending, 0.5–2 dm tall, hispid or sparingly strigose-villous; *leaves* oblong-lanceolate, 2–4(5) cm long, 2–6 mm broad, obtuse, hispid, pustulate, the upper only slightly reduced; *inflorescence* dense, very floriferous, the spikes solitary or geminate, 5–15 cm long; *bracts* evident throughout; *calyx* in fruit 3–4 mm long, broadly ovate, the segments lanceolate, connivent, hirsute to hispid villous; *pedicels* obscure; *corolla* inconspicuous about 1 mm broad; *style* barely surpassing nutlets; *gynobase* pyramidal, shorter than nutlets; *nutlets* 4, homomorphous, triangular-ovate, 1–1.3 mm long, margins rounded, the surface tan or brownish with white tuberculations, scar triangular, conspicuously excavated.

Exposed slopes and rocky ridges, mostly on limestone or caliche. Southeastern New Mexico, western Texas, and southward into northern Mexico in the state of Nuevo León and Coahuila. March to July.

This species is closely allied to *C. albida* (H.B.K.) Johnston. There should be no confusing the two as *C. albida* has a straight erect central axis or stem while this species is much branched from the base and throughout; also the flowering times are very different: *C. mexicana* is early spring and summer, while that of *C. albida* is in July and August.

17. **Cryptantha albida** (H.B.K.) I. M. Johnston

*Myosotis albida* H.B.K. Nov. Gen. et Sp. 3: 91. Aug. 1818. (San Juan del Río, Queretaro, Mexico)

*Lithospermum ramosum* Lehm. Asperif. 2: 328. Nov. or Dec. 1818. *Eritrichium ramosum* DC.

Prodromus 10: 132. 1846. *Krynitzkia ramosa* A. Gray, Proc. Amer. Acad. Arts 20: 274. 1885. C. *ramosa* E. L. Greene, Pittonia 1: 115. 1887. (Type probably came from San Juan del Río, Mexico)

Erect annual herb; *stems* single or more commonly several, with numerous loosely ascending branches, the main stem becoming somewhat woody or very stiffened below in age, 1.5–4 dm tall, strigose and sparingly hispid; *leaves* spathulate to spathulate-linear, usually folded, 2–3 cm long, 2–5 mm broad, acute to obtuse, dorsal surface hirsute, conspicuously pustulate, ventral surface sparsely hirsute to nearly glabrous; *inflorescence* terminal on the main stem and the numerous branches, the spikes solitary or rarely geminate, 1–6(10) cm long; *bracts* numerous, small; *calyx* in fruit 2.5–3 mm long, ovate, the segments lanceolate, connivent, unequal, hispid; *pedicels* obscure, nearly sessile; *corolla* inconspicuous, 1.5–2.5 mm broad; *style* surpassing mature nutlets about 0.5 mm; *gynobase* pyramidal; *nutlets* 4, homomorphous, triangular ovate, 1–1.3 mm long, margins rounded, the surface tan or brownish, with low whitish tuberculations, scar triangular, occupying much of ventral face, excavated.

Slopes, canyons, and ridges of volcanic or limestone origin. Southeastern Arizona, possibly in extreme southern New Mexico. Occurring in Trans-Pecos Texas and south in Mexico in the states of Sonora, western Coahuila, Chihuahua, Durango, and Queretaro, as well as northwestern Argentina.

The species just enters our area in southeastern Cochise County, Arizona, but may be expected in the Guadalupe Mountains of southern New Mexico.

### 18. **Cryptantha muricata** (H. & A.) Nels. & Macbr.

*Myosotis muricata* H. & A. Bot. Beecheys Voy. 369. 1840. *C. muricata* Nels. & Macbr. Bot. Gaz. 61: 42. 1916. (*Douglas*, without locality)

*Eritrichium muriculatum* A. DC. Prodromus 10: 132. 1846.

*Krynitzkia muriculata* A. Gray, Proc. Amer. Acad. Arts 20: 273. 1885. *C. muriculata* E. L. Greene, Pittonia 1: 113. 1887. (Type not given)

*C. horridula* E. L. Greene, Pittonia 5: 55. 1902. (*Mrs. Curran*, Salinas River, California, 1885)

*Krynitzkia denticulata* E. L. Greene, Bull. Calif. Acad. Sci 1: 205. 1885. *C. denticulata* E. L. Greene, Pittonia 1: 114. 1887. (*Curran*, western Nevada, 1884)

*C. densiflora* Nels. & Kenn. Proc. Biol. Soc. Wash. 19: 156. 1906. (*Kennedy* 952, Verdi, Nevada, 1904)

Moderately tall erect annual herbs; *stems* single or several, 1–10 dm tall, ascendingly few to several branched, hirsute also somewhat strigose; *leaves* linear to linear-oblanceolate, 1–5(9) cm long, 1–3(4) mm wide, acute, villous-hirsute, inconspicuously pustulate; *inflorescence* terminating the main stem and branches, the spikes geminate to quinate, 2–15 cm long; *bracts* lacking; *calyx* in fruit 2–4 mm long, ovate, deciduous, the segments lanceolate, very connivent, midrib slightly thickened and tawny-hirsute, the margins hispid; *pedicels* obscure; *corolla* inconspicuous to conspicuous, 1–7 mm broad; *style* usually much surpassing the nutlets or rarely slightly shorter than them; *gynobase* linear subulate; *nutlets* 4, homomorphous, broadly ovate, 1.5–2.5(3) mm long, lucid or dull, muricate or tuberculate, also sometimes granulate, margins acute to rounded, base truncate, scar narrow and nearly closed but at the base broadly forking and with a very small areola.

Dry gravelly bajadas and washes, or mountain slopes. Southern California from the transition zone to arid desert zone and eastward to Nevada and Arizona. April to July.

Two rather well-defined varieties occur within the area of our flora, the typical variety has conspicuous corollas 2–6 mm broad, while variety *denticulata* (E. L. Greene) Johnston has inconspicuous corollas 1–2 mm broad; otherwise the plants are quite the same. Two other varieties may occur within our area, variety *jonesii* (Gray) Johnston, and variety *clokeyi* (Johnston) Jepson.

### 19. **Cryptantha intermedia** (A. Gray) E. L. Greene

*Eritrichium intermedium* A. Gray, Proc. Amer. Acad. Arts 17: 225. 1882. *Krynitzkia intermedia* A. Gray, Proc. Amer. Acad. Arts 20: 273. 1885. *C. intermedia* E. L. Greene, Pittonia 1: 114. 1887. (*Nevin*, Los Angeles, California 1880–1882)

*C. quentinensis* Macbride. Contr. Gray Herb. 56: 58. 1918. (*Palmer 608*, San Quentin Bay, California)

*C. barbigera* var. *fergusonae* Macbr. Ibid. 59. 1918. (*Ferguson 42*, Palm Springs, California)

*C. intermedia* var. *johnstonii* Macbr. Ibid. 59. 1918. (*Johnston 1938*, Claremont, California)

Erect annual herbs; *stems* 1–several, erectly branched, 1.5–5 dm tall, very hirsute with spreading or ascending hairs, also strigose; *leaves* lanceolate to linear, acute to obtuse, 2–6(7.5) cm long, 1–5(7) mm wide, hirsute or strigose, minutely pustulate; *inflorescence* open and lax, the spikes geminate to quinate, mostly ternate, 1–15 cm long; *bracts* lacking; *calyx* in fruit (2)4–6 mm long, ovate-oblong, ascending, the segments lance-linear, connivent with spreading tips, midrib moderately thickened and very hirsute, margins strigose or hispid villous; *pedicels* obscure, 0.5 mm long; *corolla* conspicuous, 3–6(8) mm broad; *style* subequal to the nutlets, or slightly longer or shorter than them; *gynobase* linear-subulate; *nutlets* usually 4, or somewhat less by abortion, homomorphous, lanceolate to ovate, 1.8–2.3 mm long, surface muricate to tuberculate, grayish or tannish, somewhat granulate also, margins mostly obtuse, scar narrow and linear, or closed but with a small areola at the base.

Dry sandy slopes and hillsides. Northern California to northern Baja California mostly west of the Sierra Nevada Mountains but entering the desert edge along the eastern foothills. March to July.

*Cryptantha intermedia* is a highly variable species and tends to intergrade quite completely with *C. barbigera* in our area, and to a lesser extent also with *C. nevadensis*. The larger corolla of *C. intermedia* will usually separate it from its close relatives.

20. **Cryptantha decipiens** (M.E. Jones) Heller

*Krynitzkia decipiens* M. E. Jones Contr. W. Bot. 12: 6. 1910. *C. decipiens* Heller, Muhlenbergia 8: 48. 1912. (*M. E. Jones*, Yucca, Arizona, 14 May 1884)

Slender erect annual herbs; *stems* ascendingly branched throughout, 1–4(5) dm tall, strigose rarely sparsely hirsute; *leaves* mostly basal, reduced upward, linear, 1–4 cm long, 1–3(4) mm broad, obtuse to acutish, strigose and sparsely hispid, sparsely but evidently pustulate; *inflorescence* open, the spikes geminate or occasionally ternate or solitary, slender, usually densely flowered, 3–10(14) cm long; *bracts* lacking; *calyx* in fruit 2–5 mm long, ovate to oblong, strictly ascending, asymmetrical, the segments lance-linear, conspicuously connivent with spreading or recurving tips, the midrib moderately thickened and hirsute, margins strigose or weakly hirsute, the abaxial lobe usually slightly the longest; *pedicels* obscure or lacking; *corolla* minute to evident, 0.8–3.5 mm broad; *style* short, much surpassed by nutlets; *gynobase* short pyramidal; *nutlet* 1 or rarely 2, next abaxial calyx lobe, ovate-lanceolate, 1.5–2.4 mm long, margins rounded, the surface brownish, muricate to tuberculate, scar narrowly linear, but opening at base to form a small areola.

Sandy, gravelly, or rocky slopes or hillsides, often growing on limestone. Inyo and Kern counties, California, south to northern Mexico, and eastward through southern Nevada to Washington county, Utah, and western Arizona. March to May.

21. **Cryptantha recurvata** Coville

*C. recurvata* Coville, Contr. U. S. Natl. Herb. 4: 165. 1893. (*Coville & Funston 713*, Surprise Canyon, Panamint Mountains, California)

Sprawling annual herbs; *stems* slender, ascendingly branched just above the dye-stained root, 1–3 dm tall, strigose rarely hispidulose; *leaves* remote, oblanceolate or linear-oblanceolate 1–2(3.5) cm long, 1–4(5) mm broad, rounded or obtuse, strigose, inconspicuously pustulate; *inflorescence* open, the spikes solitary or geminate, slender, 2–10(12) cm long; *bracts* lacking; *calyx* in fruit 3–4 mm long, conspicuously asymetrical, bent and strongly recurved, tardily deciduous, the segments linear, the abaxial the longest, midrib moderately thickened and hirsute, the margins appressed hirsute or strigose; *pedicels* lacking; *corolla* minute, shorter than the calyx; *style* much shorter than nutlet; *gynobase* short and slender; *nutlet* 1, persistent, next abaxial calyx-lobe, lanceolate, incurved ca. 2 mm long, the tips attenuate-acute, margins obtuse, the surface dull brownish, granulate or muriculate, scar narrowly linear or closed above, below opening into a small basal areola.

Sandy or occasionally gravelly washes or slopes. Southeastern Oregon south to Inyo county, California, in the Panamint Mountains and eastward to San Juan County, Utah, and Mohave County, Arizona. April to June.

22. **Cryptantha echinella** E. L. Greene

*C. echinella* E. L. Greene, Pittonia 1: 115. 1887. *C. ambigua* var. *echinella* Jepson & Hoover, Fl. Calif. 3: 336. 1943. (*Sonne*, Mount Stanford, above Donner Lake, California 2640 m, 1886)

Annual herbs; *stems* simple below, branched above, with ascending branches, 1–3(4) dm tall, setose or occasionally strigose or hispid; *leaves* linear to oblance-linear, 1–4(6) cm long, 1–3(4.5) mm broad, obtuse, hispid, pustulate; *inflorescence* open, the spikes slender, solitary or geminate, 1–5 cm long; *bracts* evident only near the base; *calyx* in fruit 4–6 mm long, oblong-ovate, deciduous, spreading, the segments linear-lanceolate, connivent with spreading tips, midrib moderately thickened and hirsute, the margins hispid or strigose; *pedicels* obscure, about 0.5 mm long; *corolla* minute, 1–2 mm broad; *style* slightly surpassed by the nutlets; *gynobase* narrow, two-thirds as long as nutlets; *nutlets* 4, homomorphous, ovoid, 2–2.2 mm long, margins rounded, the surface finely muriculate or granulate, or verrucose, scar very narrowly linear or closed, broadly forked at the base.

Open dry ridges and slopes in the upper arid transition zone, associated with *Juniperus, Pinus,* and *Artemisia*. Sierra Nevada Mountains of California eastward to the Charleston Mountains, Nevada, with an isolated collection in northwestern Colorado, Moffatt County. *Weber* and *Salamun 12612.* June to August.

23. **Cryptantha barbigera** (A. Gray) E. L. Greene

*Eritrichium barbigerum* A. Gray, Synop. Fl. No. Amer. 2: 194. 1878. *Krynitzkia barbigera* A. Gray, Proc. Amer. Acad. Arts 20: 273. 1885. *C. barbigera* E. L. Greene, Pittonia 1: 114. 1887. (*Parry 171,* Washington County, Utah)

*Krynitzkia mixta* M. E. Jones, Contr. W. Bot. 13: 6. 1910. (*M.E. Jones 5106,* St. George, Washington County, Utah)

Erect annual herbs; *stems* 1–several, erectly branched, hirsute, 1–4(5) dm tall; *leaves* oblong to lance-linear, obtuse, 1–5(7) cm long, 3–7(13) mm wide, hirsute, inconspicuously pustulate; *inflorescence* terminating the main stem and branches, the spikes usually geminate, sometimes solitary or ternate, 2–11(16) cm long; *bracts* lacking; *calyx* in fruit 4–8(10) mm long, oblong-lanceolate, ascending, the segments lance-linear, with the tips spreading or recurving, midrib moderately thickened and hirsute, the margins long white-villous; *pedicels* obscure, 0.5–0.8 mm long; *corolla* inconspicuous, 1–2 mm broad; *style* subequal to nutlets or slightly longer; *gynobase* linear; *nutlets* 1–4, homomorphous, lanceolate, 1.5–2.5 mm long, margins rounded or slightly angled, the surface verrucose, brownish, scar linear-lanceolate, broadened at the base into a narrowly triangular areola.

Dry slopes, wash bottoms, and hillsides. Very common throughout most of the desert southwest from southeastern California and northern Baja California east through southern Nevada to southwestern Utah, Arizona, and southern New Mexico into Sonora Mexico. February to May.

24. **Cryptantha nevadensis** Nels. & Kenn.

*Krynitzkia barbigera* var. *inops* Brandg. Zoe 5: 228. Sept. 1906. *C. nevadensis* Nels. & Kenn. Proc. Biol. Soc. Wash. 19: 157. Nov. 1906. *C. barbigera* var. *inops* Macbr. Proc. Amer. Acad. Arts 51: 548. 1916. (*T. Brandegee* s.n. Mohave Desert.)

*C. arenicola* Heller, Muhlenbergia 2: 242. Dec. 1906. (*Heller* 8203, Laws, 3 miles west, Inyo Co., Calif.)

*C. leptophylla* Rydb. Bull. Torrey Club 36: 678. 1909. (*Palmer 350,* St. George, Utah.)

*C. nevadensis* var. *rigida* I. M. Johnst. Contr. Gray Herb. 74: 68. 1925. (*Pringle,* hills bordering the Mohave Desert, California, 1882)

Erect or ascending annual herbs; *stems* 1–several, slender, often flexuous, laxly branched, 1–5 dm tall, closely appressed strigose, or rarely sparsely hirsute; *leaves* linear-oblanceolate to linear, acute to obtuse, 1–4 cm long, 1–5(7) mm broad, sparsely appressed hispid, moderately pustulate; *inflorescence* lax to somewhat glomerate, spikes geminate or ternate, congested or elongate, 2.5–15 cm long; *bracts* lacking or occasionally bracted at base; *calyx* in fruit, 4–10(12) mm long, lanceolate, ascending, the segments linear-lanceolate, connivent with slender recurving tips, midrib thickened and hirsute, margins villous-setose; *pedicels* obscure about 0.5 mm long; *corolla* minute, 1–2 mm broad; *style* subequal to nutlets or a trifle shorter; *gynobase* linear about three-fourths length of nutlets; *nutlets* 4, homomorphous, lanceolate, 2–2.9 mm long, the margins obtuse, the surface mostly verrucose or somewhat muriculate near the tip, scar narrowly open and linear to nearly closed, but always with a small areola near the base.

Dry bajadas, washes, and open hillsides mainly in the *Larrea* community. The stems often supported by other vegetation. Southeastern California, northern Baja California, and eastward through Nevada to southwestern Utah and Arizona. March to May.

25. **Cryptantha gracilis** Osterh.

  *C. gracilis* Osterh. Bull. Torrey Club 30: 236. 1903. (*Osterhout* 2589, Glenwood Springs, Garfield Co., Colorado)

  *C. hillmanii* Nels. & Kenn. Proc. Biol. Soc. Wash. 19: 257. 1906. *C. gracilis* var. *hillmannii* Munz & Johnst. Bull Torrey Club 49: 39. 1922. (*Hillman*, Huffaken Ranch near Reno, Nevada)

Slender erect annual herbs; *stems* 1–several, sparsely branched from the base and above, 1–2(4) dm tall, densely short setose; *leaves* mostly basal, scattered above, linear-oblong, to narrowly oblanceolate, 1–3 cm long, 1–2(3) mm wide, rounded or obtuse, setose or weakly hispid, inconspicuously pustulate; *inflorescence* open, the spikes solitary or geminate, usually glomerate, 1–2 cm long; *bracts* lacking; *calyx* in fruit 2–3 mm long, ovate, spreading, early deciduous, the segments lanceolate, midrib slightly thickened and inconspicuously setose, the margins densely setose-villous, often tawny; *pedicels* lacking; *corolla* minute, less than 1 mm broad; *style* two-thirds to three-fourths length of nutlet; *gynobase* about half height of nutlet; *nutlets* 1 or rarely 2 or 3, homomorphous, lanceolate, 1.5–2 mm long, margins mostly rounded, surface smooth and shiny, scar linear very narrowly open at least at the base.

Dry slopes and open areas in the upper Transition Zone. Southern Idaho south through Nevada to Inyo County, California, and east to western Colorado, and northern Arizona. April to July.

*C. gracilis* enters our area from the north, and is found only on some of the higher ranges in the Mohave Desert (Charleston Mountains and the Virgin Mountains). The species never truly grows on the dry desert lowlands.

26. **Cryptantha mohavensis** E. L. Greene

  *Krynitzkia mohavensis* E. L. Greene, Bull. Calif. Acad. Sci. 1: 207. 1885. *C. mohavensis* E. L. Greene, Pittonia 1: 120. 1887. (*Curran*, Mohave Desert, California, 1884)

  *C. fallax* E. L. Greene, Pittonia 5: 54. 1902. (*E. L. Greene*, mountains above Tehachapi, California, 22 June 1889)

Usually erect annual herbs; *stems* many branched, 1–4 dm tall, short-hispid to hispid -strigose; *leaves* linear to linear-lanceolate, 1–4 cm long, 1–3 mm broad, strigose or appressed setose, minutely and densely pustulate, obtuse; *infloresence* crowded, the spikes ternate or geminate, usually dense, 2–6 cm long; *bracts* lacking; *calyx* in fruit 3–5 mm long, oblong-ovate, ascending, deciduous, the segments lanceolate, connivent, midrib moderately thickened and often sparsely hirsute, margins commonly silky-strigose; *pedicels* obscure, ca. 0.5 mm long; *corolla* conspicuous 4–7 mm broad; *style* evidently surpassing nutlets; *gynobase* columnar subulate, three-fourths height of nutlet; *nutlets* 4, homomorphous, lance-ovate to lance-oblong, 2–2.5 mm long, margins angled and obtuse near apex, surface smooth and shiny, rarely granulate, the dorsal side flat or low convex, scar closed above but opening to form a small triangular areola at the base.

Dry sandy soils. Southeastern and southern California from Inyo and Kern counties southward to the San Gabriel Mountains and Sierra Libre. May to June.

The species just enters our flora along the western boundary of the foothills of the Sierra Nevada near Bishop south to the town of Mohave, California.

27. **Cryptantha fendleri** (A. Gray) Greene

  *Krynitzkia fendleri* A. Gray, Proc. Amer. Acad. Arts 20: 268. 1885. *C. fendleri* Greene, Pittonia 1: 120. 1887. (*Fendler*, without locality, New Mexico, 1847)

  *C. ramulosissima* A. Nels. Erythea 7: 68. 1899. (*Nelson* 5275, Laramie, Wyoming)

  C. wyomingensis Gandoger, Bull. Soc. Bot. Fr. 65: 62. 1918. (*Nelson 1523*, Cummins, Wyoming)

Erect annual herbs; *stems* solitary with many divaricate or ascending lateral branches, 1–5 dm tall, densely spreading hispid; *leaves* narrowly oblanceolate, acute to nearly obtuse, 1–5 cm long, (1)2–4 mm broad, hispid, pustulate on the dorsal surface, much less so above; *inflorescence* broad, the spikes solitary or geminate 2–13 cm long, loosely flowered; *bracts* lacking or rarely 1 or 2 near the base; *calyx* in fruit 3–6(7.5) mm long, oblong-lanceolate, ascending the segments linear to lance-linear, slightly connivent with the tips slightly spreading, midrib thickened and hirsute, margins strigose; *pedicels* about 0.5 mm long, obscure; *corolla* inconspicuous, about 1 mm broad; *style* subequal to or slightly exceeding the nutlets; *gynobase* subulate, about two-thirds height of nutlets; *nutlets* 4, or sometimes fewer by abortion, homomorphous, lanceolate, the tips acuminate, 1.5–2 mm long, margins obtuse or rounded, surface smooth and usually shiny, scar closed or slightly open above, below forming a triangular areola.

Open, exposed, usually sandy sites in the *Artemisia* and *Juniperus* associations, 3,500–7,000 feet elevation. Southeastern Washington and northeastern Oregon east to southern Alberta and Saskatchewan to eastern Nebraska, northern New Mexico, and Arizona. June to August.

28. **Cryptantha flava** (A. Nels.) Payson

*Oreocarya flava* A. Nels. Bull. Torrey Club 25: 202. 1898. *C. flava* Payson, Ann. Mo. Bot. Gard. 14: 259. 1927. (*A. Nelson 3074*, point of rocks, Sweetwater County, Wyoming, 1 June 1897)

*O. lutescens* E. L. Greene, Pittonia 4: 93. 1899. *C. confertiflora* var. *lutescens* Brand, Pflanzenr. IV. (Heft. 97) 252: 90. 1931. (*C. F. Baker*, hills about Aztec, New Mexico, 25 April 1899)

Perennial herbs; *stems* many from a multiple caudex, 1.3–4 dm tall, densely long white-hairy at the base, becoming setose and strigose upward; *leaves* narrowly oblanceolate to nearly linear, acute, 2–9 cm long, 3–8 mm wide, dorsal surface strigose and appressed setose with pustulate hairs, ventral surface almost uniformly strigose, and with the pustules less conspicuous; *inflorescence* narrow to somewhat open, 0.5–2.5 dm long, conspicuously yellow setose; *bracts* inconspicuous; *pedicels* 3–5 mm long in fruit; *calyx* 8–10 mm long in anthesis, in fruit becoming 9–12 mm long, the segments linear, densely setose, with yellowish hairs; *corolla* yellow, the tube 9–12 mm long, crests at base of tube absent or nearly so, fornices yellow, truncate, emarginate, 1–1.5 mm long, limb 8–10 mm broad; *style* exceeding mature fruit 3–7 mm (heterostyled); *nutlets* lanceolate, 3.4–4 mm long, 1.9–2.2 mm wide, 1 or 2 usually maturing, the margins acute, in contact when more than 1 nutlet matures, both surfaces of nutlet smooth and glossy, scar straight, closed, elevated margin lacking.

Dry sandy soil often in dune areas, 4,000–7,000 feet elevation. Southwestern Wyoming, south through eastern Utah and western Colorado into northeastern Arizona and northwestern New Mexico. April to August.

29. **Cryptantha confertiflora** (Greene) Payson

*Krynitzkia leucophaea* var. *alata* M. E. Jones, Proc. Calif. Acad. Sci. 5: 710. 1895. *Oreocarya alata* A. Nels. Coulter and Nelson, Man. Cent. Rocky Mts. 417. 1909. (*M. E. Jones 5144*, on sandstone cliffs, Silver Reef, Utah, 3 May 1894)

*Oreocarya confertiflora* E. L. Greene, Pittonia 3: 112. 1896. (S. *B. Parish 1316*, Cushenberry Springs on the north side of the San Bernardino Mountains, San Bernardino County, California, 1882)

*O. lutea* E. L. Greene, Muhlenbergia 2: 240. 1906. name only, Feddes Repert. Spec. Nov. Regni. Veg. 19: 72. 1923. description. (A. A. *Heller 8211*, White Mountains, Inyo County, California, 9 May 1906)

Perennial herbs; *stems* 1–7, slender, 1.7–4.3 dm tall, tomentose at base, strigose and setose upward; *leaves* linear to oblanceolate, 3–12 cm long, 2–10(16) mm wide, acute, dorsal surface densely strigose and appressed setose with pustulate bases, ventral surface uniformly strigose and with few or no pustules; *inflorescence* subcapitate, 0.3–2 dm long, strigose, and with flattened, twisted, setose hairs; *bracts* inconspicuous; *calyx* in anthesis 6–8 mm long, in fruit becoming 10–14 mm long, the segments linear-lanceolate, strigose and spreading setose; *corolla* yellow, the tube 9–13 mm long, fornices broad, emarginate, about 1 mm long, crest at base of tube evident or sometimes lacking, limb 8–10 mm wide; *heterostyled*; *nutlets* ovate or triangular-ovate, 3.5–4 mm long, 2.5–3 mm wide, usually all four maturing, margins narrowly winged, in contact, both surfaces smooth and glossy, scar straight, closed, and lacking an elevated margin.

Dry exposed sites on a wide variety of soil types. Southeastern California, eastward through southern Nevada into northern Arizona and southern Utah. April to July.

A tall handsome plant closely related to *C. flava* but having nearly capitate inflorescences and broadly ovate nutlets. The yellow flowers also tend to be lighter in color or a washed out yellow.

30. **Cryptantha capitata** (Eastw.) I. M. Johnston

*Oreocarya capitata* East. Leaflets W. Bot. 1: 9. 1937. *C. capitata* I. M. Johnst. J. Arnold Arbor 21: 66. 1940. (A. *Eastwood 5969*, Hermit Trail on the south rim of the Grand Canyon, Coconino County, Arizona, 9 April 1917)

Erect perennial herbs; *stems* weak, 1–several, 1.5–2.7 dm tall, appressed setose; *leaves* linear or narrowly oblanceolate, 3–8 cm long, 3–5 mm wide, dorsal surface appressed setose-pustulate, ventral surface uniformly strigose and without pustules; *inflorescence* capitate, or with one or two glomerules below the terminal cluster, 0.1–0.4(7) dm long, spreading white-setose; *calyx* 7–9 mm long in anthesis, in fruit becoming 11–16 mm long, the segments linear-lanceolate, conspicuously setose-pustulate; *corolla* white, the tube 9–12 mm long, fornices yellow, emarginate, about 1 mm long, papillose, crests at base of tube conspicuous, limb 6–8 mm wide; *style* exceeding mature fruit 4–5 mm; *nutlets* lanceolate, 4–5 mm long, 2–3 mm wide, two to four usually maturing, the margins in contact, knifelike, both surfaces glossy-smooth, scar closed, straight, and without an elevated margin.

Open or exposed somewhat sandy soils in the Transition Zone, 6,500 to 8,500 feet elevation. South central Utah and north central Arizona in the Colorado River drainage basin. April to July.

In our area this species is restricted to the Grand Canyon National Park along the Kaibab and Hermit trails, both on the north and south rims.

31. **Cryptantha fulvocanescens** (S. Wats.) Payson

*Eritrichium glomeratum* var. *fulvocanescens* S. Wats. Bot. King Exp. 243. 1871. *E. fulvocanescens* A. Gray, Proc. Amer. Acad. Arts 10: 61, 1875. *Krynitzkia fulvocanescens* A. Gray, Proc. Amer. Acad. Arts 20: 280. 1885. *Oreocarya fulvocanescens* E. L. Greene, Pittonia 1: 58. 1887. *C. fulvocanescens* Payson, Ann. Mo. Bot. Gard. 14: 319. 1927. (*Fendler 632*, near Santa Fe, Santa Fe County, New Mexico, 1847)

*Krynitzkia echinoides* M. E. Jones, Proc. Calif. Acad. Sci. 5: 709. 1895. *Oreocarya echinoides* Macbr. Contr. Gray Herb. 48: 31. 1916. as to synonymy, not as to specimens cited. *C. echinoides* Payson, Ann. Mo. Bot. Gard. 14: 321. 1927. *C. fulvocanescens* var. *echinoides* Higgins, Great Basin Nat. 29: 30. 1969. (*M. E. Jones 5297*, Pahria Canyon, Kane County, Utah, 26 May 1894)

Densely caespitose perennials from a strongly lignified taproot; *stems* many from a multiple caudex, 0.8–3 dm tall, white hairy at the base, setose-hirsute upward; *leaves* spatulate or oblanceolate, acute to obtuse, 1.5–7 cm long, 4–12 mm wide, uniformly strigose, pustules mostly confined to the dorsal surface; *inflorescence* narrow or somewhat open at maturity, 0.3–1.9 dm long, white or yellowish setose-hispid; *bracts* inconspicuous; *pedicels* 2–10 mm long; *calyx* 4–6 mm long in anthesis, in fruit becoming 9–13 mm long, the segments linear, densely white or yellowish setose-hispid; *corolla* white, the tube 7–11 mm long, fornices yellow, emarginate or rounded, 0.7–1.3 mm long, crests at base of tube evident or lacking, limb 7–9 mm wide; *style* exceeding mature fruit 3–7 mm; *nutlets* lance-ovate, 3.5–4.5 mm long, 2–3 mm wide, one or two usually maturing, the margins acute to obtuse, in contact when more than one nutlet matures, both surfaces densely and uniformly muricate, scar open or nearly closed, elevated margin lacking.

Dry, sandy to clay soils on exposed areas in the *Artemisia* or *Juniperus-Pinus* association, 4,000 to 7,500 feet elevation. Central Utah and north central Arizona east to western Colorado and central New Mexico, with an isolated population at White Sands National Monument. April to August.

Two rather distinct varieties occur within our area and may be separated by the following key:

1. Murications on the nutlet rounded; corolla 9–13 mm long; inflorescence narrow, white setose at maturity; usually growing on sandy soils .................................................................................................................... var. *fulvocanescens*
— Murications on the nutlet with one or two setose projections; corolla 7–9 mm long; inflorescence broader and usually yellowish setose-hispid at maturity; usually growing on clay soils ........................................ var. *echinoides* (Jones) Higgins

The variety *echinoides* is limited in our area to north central Arizona and northeastern New Mexico.

32. **Cryptantha oblata** (M. E. Jones) Payson

*Krynitzkia oblata* M. E. Jones, Contr. W. Bot. 13: 4. 1910. *Oreocarya oblata* Macbr. Proc. Amer. Acad. Arts 51: 548. 1916. *Hemisphaerocarya oblata* Brand, Feddes Repert. Spec. Nov. Regni Veg. 24: 61. 1927. *C. oblata* Payson, Ann. Mo. Bot. Gard. 14: 254. 1927. (*M. E. Jones 3579*, El Paso, Texas, 23 April 1884)

*O. hispidissima* Wooton & Standl. Contr. U. S. Natl. Herb. 19: 545. 1915. not *O. hispidissima* (Torr.) Rydb. (*Wright 1566*, near El Paso and Dona Ana, March to April)

Perennial or biennial herb; *stems* several, 1–3.5 dm tall, retrorsely setose and spreading hirsute; *leaves* oblanceolate, acute, 3–10 cm long, 4–14 mm wide, coarsely strigose and setose dorsally with conspicuous pustules, ventral surface weakly strigose-setose, and with fewer pustulate hairs, the petioles ciliate-margined; *inflorescence* somewhat open, especially in age, 0.3–2 dm long, setose-hirsute; *calyx* 5–7 mm long in anthesis, becoming 8–10 mm long in fruit, the segments linear-lanceolate, densely setose-hirsute; *corolla* white, tube 7–10 mm long, crests at base of tube lacking, fornices yellow, broad, papillose, limb 8–12 mm wide; *style* 3–5 mm longer than mature fruit; *nutlets* ovoid, usually all four maturing, the margins narrowly separated, acute, 2.5–3 mm long, 2–2.5 mm wide, dorsal surface rugose-tuberculate, ventral surface smooth or slightly uneven, scar closed, straight, and without an elevated margin.

Sandy or gravelly to rocky hillsides mostly on gypsum soils, 1,000 to 5,000 feet elevation. South central New Mexico south through Trans-Pecos Texas into northern Mexico. March to September.

This species is only one of the many gypsophilous plants that occur in the southeastern part of our area.

33. **Cryptantha paysonii** (Macbr.) I. M. Johnston

*Oreocarya paysonii* Macbr. Contr. Gray Herb. 48: 36. 1916. *Hemisphaerocarya paysonii* Brand, Feddes Repert. Spec. Nov. Regni. Veg. 24: 61. 1927. *C. paysonii* I. M. Johnst. Wrightia 2: 160. 1961. (*O. B. Metcalfe 1576*, limestone hills at Berendo Creek, Sierra County, New Mexico, 12 May 1905)

Caespitose perennials; *stems* erect, stout, (0.5)1.6–2.9 dm tall, strigose and more or less spreading setose; *leaves* oblanceolate, obtuse to acute, 3–9 cm long, 5–15 mm wide, dorsal surface finely strigose or subtomentose, also setose with pustulate hairs, ventral surface similar but with fewer pustulate hairs; *inflorescence* subcapitate, consisting of four to six compact cymules, 0.5–1.2 dm long, setose; *calyx* 7–9 mm long in anthesis, becoming 9–10 mm long in fruit, the segments linear-lanceolate, setose; *corolla* white to yellowish tinged, the tube 12–14 mm long, crests at base of tube lacking, fornices yellow, rounded, densely papillose, 0.5–1 mm long, limb 10–13 mm wide; *heterostyled*; *nutlets* ovate, 2.7–3 mm long, 2–2.5 mm wide, usually all four nutlets maturing, margins narrowly winged, in contact, both surfaces finely rugulose or finely tuberculate, scar closed, straight, lacking an elevated margin.

Gravelly or rocky hillsides mostly on gypsum or limestone soils, 4,000–7,500 feet elevation. Southeastern New Mexico and Trans-Pecos Texas in Culberson County. April to June.

34. **Cryptantha paradoxa** (A. Nels.) Payson

*Oreocarya paradoxa* A. Nels. Bot. Gaz. 56: 69. 1913. *C. paradoxa* Payson, Ann. Mo. Bot. Gard. 14: 330. 1927. (*E. P. Walker 91*, dry gypsum hills in Paradox Valley, Montrose County, Colorado, 17 June 1912)

*O. gypsophila* Payson, Bot. Gaz. 60: 380. 1915. (*Payson 458*, dry gypsum hills in Paradox Valley, Colorado, 18 June 1914)

Small perennial herbs; *stems* 1–several, slender, 0.4–1.2 dm tall, subtomentose near the base, weakly setose above; *leaves* oblanceolate to spatulate, usually folded, obtuse, 1.5–4 cm long, 2–4(7) mm wide, dorsal surface with appressed setose-pustulate hairs, ventral surface uniformly strigose and without pustulate hairs, the petioles ciliate-margined; *inflorescence* subcapitate, 0.1–0.4 dm long, setose; *bracts* inconspicuous; *calyx* in anthesis 5–6 mm long, in fruit becoming 6–8 mm long, the segments linear-lanceolate, weakly setose; *corolla* white with a yellow tube 10–12 mm long, crests at base of tube lacking, fornices yellow, broad, slightly emarginate, papillose, 0.5 mm long, limb 10–12 mm wide; *style* exceeding mature fruit 4–9 mm; *nutlets* lanceolate, turgid, 2–3 mm long, 1.3–1.6 mm wide, all four usually maturing, margins acute to obtuse, not in contact, dorsal surface densely tuberculate and conspicuously rugose, ventral surface tuberculate, also somewhat rugulose, scar open, constricted below the middle, the margin elevated.

Dry, sandy, gravelly, or clay soils, 4,000 to 7,500 feet elevation. Emery County, Utah, western Colorado, and San Juan County, New Mexico. May to June.

In our area known only from one collection by *Duane Atwood 2527*, 12 miles west of Shiprock on Hwy 504, 15 May 1970.

35. **Cryptantha bakeri** (E. L. Greene) Payson

*Oreocarya bakeri* E. L. Greene, Pittonia 4: 92. 1899. *C. bakeri* Payson, Ann. Mo. Bot. Gard. 14: 331. 1927. (*Baker, Earle,* and *Tracy 827*, Mancos

River sage plains in southern Colorado, 8 July 1898)

*O. eulophus* Rydb. Bull. Torrey Club 31: 637. 1904. (*Crandall*, Delores, Colorado, 1892)

Biennial or short-lived perennials; *stems* stout, 1–3 dm tall, spreading setose-hirsute; *leaves* oblanceolate, obtuse, mostly basal, 3–6 cm long, 5–12 mm wide, dorsal surface strigose and spreading setose, pustulate, ventral surface uniformly strigose and with few or no pustulate hairs; *inflorescence* narrow, 0.6–2.5 dm long, setose-hirsute; *bracts* evident, slightly surpassing the individual cymes; *calyx* in anthesis 3.5–4 mm long, in fruit becoming 6–8 mm long, the segments broadly lanceolate or ovate, conspicuously setose; *corolla* white, the tube 4–6 mm long, crests at base of tube lacking, fornices yellow, emarginate, 1–1.5 mm long, limb 6–8 mm wide; *style* exceeding mature fruit 1–2 mm; *nutlets* ovate-lanceolate, 2.5–3 mm long, 1.5–2 mm wide, three to four usually maturing, margins obtuse, nearly in contact, dorsal surface deeply and sharply rugose, ventral surface tuberculate and short rugose, scar closed, surrounded by a definitely elevated white margin.

Dry sandy or clay soils in *Pinyon-Juniper* community 4,000 to 8,000 feet elevation. Southeastern Utah, northeastern Arizona in Apache and Navajo counties, and Southwestern Colorado. May to August.

A species closely allied with *C. flavoculata* but having a shorter style and corolla, and the nutlet scar tightly closed.

36. **Cryptantha flavoculata** (A. Nels.) Payson

*Oreocarya flavoculata* A. Nels. Erythea 7: 66. 1899. *C. flavoculata* Payson, Ann. Mo. Bot. Gard. 14: 334. 1927. (*A. Nelson 4572*, Piedmont, Wyoming, 7 June 1898)

*O. flavoculata spatulata* A. Nels. Erythea 7: 67. 1899. (*A. Nelson 2977*, gravelly hilltops near Evanston, Wyoming, 29 May 1897)

*O. cristata* Eastw. Bull. Torrey Club 30: 244. 1903. (*Eastwood*, Grand Junction, Colorado, 17 May 1893)

*O. shockleyi* Eastw. Bull. Torrey Club 30: 245. 1903. (*Shockley 244*, Miller Mountain, Esmeralda County, Nevada)

*O. eastwoodae* Nels. & Kenn. Muhlenbergia 3: 141. 1908. (*Kennedy & Goodding 146*, Mormon Mountains, Lincoln County, Nevada)

Caespitose perennial herbs; *stems* 1–several, slender, 1–3.7 dm tall, strigose and spreading setose with slender bristles; *leaves* linear-oblanceolate to spatulate, obtuse or sometimes acute, 3–11 cm long, 3–15 mm wide, densely strigose and weakly setose, dorsal surface conspicuously pustulate, ventral surface with few pustules and sometimes silky-strigose; *inflorescence* narrow, or sometimes slightly open and lax, 0.5–3 dm long; *bracts* evident but not conspicuous; *calyx* 5–6 mm long in anthesis, in fruit becoming 8–10 mm long, the segments lanceolate to ovate; *corolla* white or pale yellow, the tube usually yellow, 7–10 mm long, crests at base of tube lacking, fornices yellow, minutely papillose, 1–2 mm long, limb 8–12 mm wide; *style* exceeding mature fruit 4–8 mm (heterostyled); *nutlets* lanceolate to lance-ovate, 2.5–3.5 mm long, 1.8–2 mm wide, usually all four maturing, margins obtuse, in contact or slightly separated, dorsal surface muricate, tuberculate, and with conspicuous ridges, sometimes nearly foveolate, ventral surface tuberculate, rarely with ridges, scar open, constricted near the middle and surrounded by a high, elevated margin.

On a wide variety of soils mostly in the *Pinyon-Juniper* community, but also occurring in the *Artemisia* and the *Spruce-Fir* communities, 3,000–8,500 feet elevation. East central California eastward through Nevada and Utah into southwestern Wyoming, western Colorado, and northern Arizona. April to July.

37. **Cryptantha tenuis** (Eastw.) Payson

*Oreocarya tenuis* Eastw. Bull. Torrey Club 30: 244. 1903. *C. tenuis* Payson, Ann. Mo. Bot. Gard. 14: 327. 1927. (*A. Eastwood*, near Moab, in Court House Wash, Grand County, Utah, 25 May 1892)

Caespitose perennial herbs; *stems* slender, 1–many, 1.3–2.5 dm tall, strigose and weakly spreading setose; *leaves* linear-spatulate, mostly basal, obtuse, 2–5 cm long, 3–6 mm wide, dorsal surface strigose and weakly spreading setose, evidently pustulate, ventral surface uniformly strigose and without pustules; *inflorescence* narrow, interrupted, 0.6–1.4 cm long, weakly setose; *bracts* inconspicuous; *calyx* 4.5–6 mm long in anthesis, in fruit becoming 7–9 mm long, the segments linear-lanceolate, white-setose; *corolla* white, somewhat campanulate, the tube 5.5–7 mm long, crests at base of tube lacking or sometimes evident, fornices yellow, broad, emarginate, papillose, limb 5–8 mm wide; *style* exceeding mature fruit 3–4 mm; *nutlets* lanceolate, 3–4 mm long, 1.8–2 mm wide, all four usually maturing, margins acute, nearly in contact, dorsal surface carinate, sharply and deeply rugose, ventral surface rugose, scar open, constricted above the base, and with an elevated margin.

Dry, sandy, or clayey exposed slopes and benches, 2,500 to 5,500 feet elevation. Southeastern Utah in Emery, Grand, Wayne, and San Juan counties. The species undoubtedly also occurs in northeastern Arizona, because several collections from San Juan County, Utah, have been made within less than a mile of the Arizona border and may have been within Arizona; it would be very hard to tell exactly where the boundary is in this remote area. April to July.

38. **Cryptantha jamesii** (Torr.) Payson

*Eritrichium jamesii* Torr. in Marcy, Expl. Red River 262. 1854. *Krynitzkia jamesii* A. Gray, Proc. Amer. Acad. Arts 20: 278. 1885 in part. (*James*, barren deserts high upon the Platte)

*E. multicaule* Torr. in Marcy, Expl. Red River 262. 1854. *Oreocarya multicaulis* E. L. Greene, Pittonia 3: 114. 1896. *O. suffruticosa* var. *multicaulis* Payson, Univ. Wyo. Pub. Bot. 1: 171. 1926. *Hemisphaerocarya suffruticosa* var. *multicaulis* Brand, Feddes Repert. Spec. Nov. Regni. Veg. 24: 60. 1927. *C. jamesii* var. *multicaulis* Payson, Ann. Mo. Bot. Gard. 14: 244. 1927. (*Fendler 636*, near Santa Fe, New Mexico, 1847) = var. *multicaulis*.

*O. abortiva* E. L. Greene, Pittonia 3: 114. 1896. *Krynitzkia multicaulis* var. *abortiva* M. E. Jones, Contr. W. Bot. 13: 5. 1910. *O. suffruticosa* var. *abortiva* Macbr. Proc. Amer. Acad. Arts 51: 547. 1916. *Hemisphaerocarya abortiva* Brand, Feddes Repert. Spec. Nov. Regni. Veg. 24: 61. 1927. *C. jamesii* var. *abortiva* Payson, Ann. Mo. Bot. Gard. 14: 250. 1927. (*S. B. Parish 3694*, Bear Valley, San Bernardino Mountains, California, 16–20 June 1895) = var. *abortiva*.

*O. cinerea* E. L. Greene, Pittonia 3: 113. 1896. *O. multicaulis* var. *cinerea* Macbr. Proc. Amer. Acad. Arts 51: 54. 1916. *O. suffruticosa* var. *cinerea* Payson, Univ. Wyo. Publ. Bot. 1: 171. 1926. *Hemisphaerocarya cinerea* Brand, Feddes Repert. Spec. Nov. Regni. Veg. 24: 61. 1927. *C. jamesii* var. *cinerea* Payson, Ann. Mo. Bot. Gard. 14: 246. 1927. (*E. L. Greene*, southern Colorado, on the plains near Pueblo, 1873) = var. *setosa*.

*O. disticha* Eastw. Bull. Torrey Club 30: 238. 1903. *C. jamesii* var. *disticha* Payson, Ann. Mo. Bot. Gard. 14: 248. 1927. (*A. Eastwood 90*, on Bartons Range, San Juan County, Utah, 13 July 1895) = var. *disticha*.

*Krynitzkia multicaulis* var. *setosa* M. E. Jones, Contr. W. Bot. 13: 4. 1910. *Hemisphaerocarya suffruticosa* var. *setosa* Brand, Feddes Repert. Spec. Nov. Regni. Veg. 24: 60. 1927. *C. jamesii* var. *setosa* I. M. Johnst. ex Tidestr. Proc. Biol. Soc. Wash. 48: 42. 1935. (*M. E. Jones*, near Fort Cove, Utah, 27 June 1901)

*O. pustulosa* Rydb. Bull. Torrey Club 40: 480. 1913. *C. pustulosa* Payson, Ann. Mo. Bot. Gard. 14: 252. 1927. *H. suffruticosa* var. *pustulosa* Brand, Feddes Repert. Spec. Nov. Regni. Veg. 24: 60. 1927. *C. jamesii* var. *pustulosa* Harrington, Man. Pl. Colorado 466, 641. 1954. (*Rydberg & Garrett 9320*, Hammond Canyon on the Elk Mountains, San Juan County, Utah, 31 July 1911) = var. *pustulosa*

*O. multicaulis* var. *laxa* Macbr. Contr. Gray Herb. 48: 35. 1916. *H. laxa* Brand, Feddes Repert. Spec. Nov. Regni. Veg. 24: 60. 1927. *C. jamesii* var. *laxa* Payson, Ann. Mo. Bot. Gard. 14: 246. 1927. (*C. G. Pringle 776*, on sand hills near Paso del Norte, Chihuahua, Mexico, 20 September 1886) = var. *laxa*.

Erect to caespitose perennials; *stems* 1–many, 1–6 dm tall, glabrous to evidently hirsute; *leaves* linear to broadly oblanceolate, obtuse to acute, 2–15 cm long, 2–15 mm wide, glabrous to hirsute, usually pustulate dorsally, ventral surface lacking pustules or the pustules very inconspicuous; *inflorescence* open, the cymules usually elongating, tomentose to setose-hirsute; *bracts* inconspicuous to very evident; *calyx* in anthesis 3–4 mm long, in fruit becoming 5–7 mm long, the segments ovate-lanceolate, subtomentose to setose-hirsute or sometime nearly glabrous; *corolla* white, the tube 2.5–3 mm long, crests at base of tube conspicuous, fornices light-yellow, emarginate, 0.5–1 mm long, limb 5–8 broad; *style* exceeding mature fruit 1–3 mm; *fruit* oblate-ovoid; *nutlets* ovate-lanceolate, 1–4 maturing, 2–2.5 mm long, 1.5–2 mm wide, the margins not in contact, acute, both surfaces smooth and glossy, scar straight, closed, extending from the base to near the apex, elevated margin lacking.

In a wide variety of habitats and on very sandy to extremely gumbo clays, 2,000 to 10,500 feet elevation. Southeastern California eastward through southern Nevada and Utah into Wyoming, South Dakota, southward through the high plains into northern Mexico, also northern Arizona and most of New Mexico. April to October.

*Cryptantha jamesii* is a wide-ranging heteromorphic species with a number of diverse growth forms. These growth forms correlated with soil types and altitudinal differences form the basis for the various varieties.

1. Ventral surface of the leaves glabrous, the petioles not ciliate margined, or tufted at the base of the plant; in our area limited to northeastern Arizona and northwestern New Mexico ........................................ var. *pustulosa* (Rydb.) Harrington

— Ventral surface of leaves strigose or setose, the petioles ciliate margined, leaves usually tufted at the base of plant ........................................ 2

2(1). Stems simple, not branched above the base ........................................ 3

— Stems branched from the base as well as above ........................................ 5

3(2). Stems 1–4.4 dm long, usually twice as long as the basal tuft of leaves; widespread variety throughout the higher elevations in Arizona and New Mexico of our area ........................................ var. *multicaulis* (Torr.) Payson

— Stems 0.2–0.9 dm long, usually not exceeding the basal tuft of leaves ........................ 4

4(3). Flora bracts exceeding the cymules; stems low, decumbent; mountains of southern California and Nevada .................................... var. *abortiva* (Greene) Payson

— Floral bracts not exceeding the cymules; stems erect or nearly so; common on *Artemisia* flats and in the Pinyon-Juniper community, in our area confined to northern Arizona and New Mexico ..................... var. *setosa* (Jones) Johnst. ex Tidestr.

5(2). Stems decumbent or ascending; plants of the great plains ......................... var. *jamesii*

— Stems erect ........................................ 6

6(5). Leaves linear; cymules 8 cm long or longer, very lax; in our area confined to sand hills in the vicinity of Las Cruces, New Mexico ........... var. *laxa* (Macbr.) Payson

— Leaves oblanceolate, cymules usually shorter than 8 cm long and more congested; in our area limited to northern Arizona and northwestern New Mexico on sandy dune areas ........................................ var. *disticha* (Eastw.) Payson

39. **Cryptantha atwoodii** Higgins

*C. atwoodii* Higgins. Southw. Naturalist 19:(2) 127–130. 1974. (*D. Atwood 2624*, 7 miles north of Junction Hwy 89/164 on Hwy 89, Coconino County, Arizona, 20 May 1970)

Biennial or short-lived perennial herbs; *stems* several, arising from the branched caudex, 0.5–3 dm tall, spreading setose with slender somewhat stiffened hairs; *leaves* oblanceolate, folded, obtuse, 1–4 cm long, 2–6 mm wide, setose on both surfaces, conspicuously pustulate on the dorsal side; *inflorescence* capitate or with several reduced clusters below the terminal cymule, 0.1–1.3 dm long; *calyx* 3–4 mm long in anthesis, in fruit becoming 5–7 mm long, the segments lanceolate, setose; *corolla* white, the tube 4–4.5 mm long, crests at base of tube lacking, fornices yellow, rounded, 0.5 mm long, limb 5–8 mm broad; *style* exceeding mature fruit 1.5–3 mm; *fruit* depressed globular; *nutlets* ovate, 1.9–2.5 mm long, 1.8–2 mm wide, usually all four maturing, margins acute, not in contact, both surfaces smooth and glossy, opaque, scar straight, closed, extending from the base to near the apex, elevated margin lacking.

Dry hillsides in shaley soil. A very narrow endemic from Coconino County, Arizona, all collections coming from the area about 7 miles south of the gap along Hwy 89. April to May.

The area in which this species grows is extremely overgrazed. It was noted that the sheep in the area also utilized this plant for food, although it is not very palatable; also the individual plants are extremely hard to find. *C. atwoodii* is one of those rare endemics that should be protected.

40. **Cryptantha palmeri** (A. Gray) Payson

*Krynitzkia palmeri* A. Gray, Proc. Amer. Acad. Arts 20: 278. 1885. *Oreocarya palmeri* Greene, Pittonia 1: 57. 1887. *Hemisphaerocarya palmeri* Brand, Feddes Repert. Spec. Nov. Regni. Veg. 24: 61. 1927. (*Palmer 895*, 40 miles south of Saltillo, Coahuila, Mexico, March 1880)

*C. coryi* I. M. Johnst. J. Arnold Arbor 20: 396. 1939. (*V. L. Cory*, s.n., about 2 miles west of Longfellow, Pecos County, Texas, 15 April 1936)

Biennial or short-lived perennials; *stems* 1–several, 1.7–4 dm tall, spreading setose or hirsute; *leaves* linear-lanceolate, acute, 3–10(16) cm long, 4–10 mm wide, strigose and subtomentose, pustulate hairs conspicuous on the dorsal surface, fewer and not evident on the ventral surface; *inflorescence* broad topped due to the elongation of the cymules in age, 0.3–2.7 dm long, setose; *bracts* inconspicuous; *calyx* 4–6 mm long in anthesis, in fruit becoming 7–10 mm long, the segments lanceolate, setose or weakly hispid; *corolla* white, the tube 4–6 mm long, crests at base of tube lacking, fornices yellow, rounded, papillose, 0.5–1 mm long, limb 7–9 mm wide; *style* exceeding mature fruit 2–3.5 mm; *nutlets* ovate, 2.5–2.8 mm long, 2–2.7 mm wide, the margins not in contact, acute, both surfaces of the nutlet smooth and glossy, scar tightly closed and without an elevated margin.

Gravelly to rock hillsides on gypsum, 1,000–4,000 feet elevation. Southeastern New Mexico, western Texas, and northern Mexico in the states of Nuevo Leon and Coahuila. April to July.

A Chihuahuan Desert species that just enters our area in southeastern New Mexico. It is found almost exclusively on gypsum or limestone soils.

41. **Cryptantha setosissima** (A. Gray) Payson

*Eritrichium setosissima* A. Gray, Proc. Amer. Acad. Arts 12: 80. 1877. *Krynitzkia setosissima* A. Gray, Proc. Amer. Acad. Arts 20: 276. 1885. *O. setosissima* E. L. Greene, Pittonia 1: 58. 1887. (*L. F. Ward 646*, at Fish Lake, Sevier County, Utah, 25 August 1875)

Biennial or short-lived robust perennial herbs; *stems* 1–3, erect, 3–10 dm tall, hirsute; *leaves* clustered at the base, reduced upward, oblanceolate, 3–13 cm long, 5–15 mm wide, setose, with some finer twisted pubescence beneath, pustulate hairs numerous on both surfaces; *inflorescence* broad topped due to the elongation of the scorpioid racemes, 1–5 dm long; *calyx* 4–6 mm long in anthesis, in fruit becoming 9–11 mm long, the segments broadly lanceolate or ovate, setose; *corolla* white, the tube 3–5 mm long, constricted above the ovary by the conspicuous ring of crests, fornices yellow, emarginate, about 0.5 mm long, limb 7–9 mm broad; *style* exceeding mature fruit 1–2 mm; *nutlets* ovate, 5–6 mm long, 3.5–4.5 mm wide, papery, with a broad winged margin, dorsal surface muricate and inconspicuously rugose or tuberculate, ventral surface smooth or nearly so, scar straight, narrow, slightly open, elevated margin lacking.

Gravelly to sandy soils in the *Pinyon-Juniper* association or the *Spruce-Fir* association, 6,000 to 11,000 feet elevation. Nye County, Nevada, eastward to central Utah and southeastward in the mountainous areas of Arizona to Greenlee County.

This is one of the most distinctive species in the entire genus, with its stout, strict, solitary stems, and its broadly winged nutlets.

42. **Cryptantha thyrsiflora** (E. L. Greene) Payson

*Eritrichium glomeratum* var. *hispidissimum* Torr. Bot. Mex. Bound. 140. 1859 in part. *O. hispidissima* Rydb. Bull. Torrey Club 33: 150. 1906. (Type not given)

*Oreocarya thyrsiflora* E. L. Greene, Pittonia 3: 111. 1896. *C. thyrsiflora* Payson, Ann. Mo. Bot. Gard. 14: 283. 1927. (*E. L. Greene*, Cheyenne, Wyoming, 6 July 1892)

*O. urticacea* Wooton & Standl. Contr. U. S. Natl. Herb. 16: 166. 1913. (*A. A. & E. G. Heller 3731*, Canyoncito, Santa Fe County, New Mexico, 18 June 1897)

*O. monosperma* Osterh. Bull. Torrey Club 46: 55. 1919. (*Osterhout 5754*, Trinidad, Las Animas County, Colorado, 20 July 1918)

Short-lived perennials or sometimes biennial; *stems* stout, 1–several, arising from the base, 1.7–4 dm tall, very hispid; *leaves* oblanceolate, obtuse, 5–12 cm long, 5–14 mm wide, spreading setose or hispid, pustulate on both surfaces; *inflorescence* very broad 1–3 cm long, 0.6–2.5 dm wide, setose or hispid; *bracts* 2–3 cm long, but hidden by the elongate cymules; *calyx* in anthesis 3–4 mm long, in fruit becoming 6–9 mm long, the segments linear, setose; *corolla* white, the tube 3–4 mm long, crests at base of tube conspicuous, fornices yellow, emarginate, papillose, about 0.5 mm long, limb 5–8 mm wide; *style* exceeding mature fruit 1–1.5 mm; *nutlets* ovate to ovate-lanceolate, 2.5–3.5 mm long, 1.5–2 mm wide, usually 2 to 4 maturing, acute, margins in contact, dorsal surface low rugulose and tuberculate, sometimes with murications between the rugae, ventral surface similar but with fewer ridges or sometimes almost smooth, scar subulate, the margin not elevated.

Plains, foothills, and mountain slopes, 4,500–9,600 feet elevation. Southeastern Wyoming and western Nebraska, south through the eastern two thirds of Colorado into northeastern New Mexico and the Oklahoma Panhandle. May to September.

This is a very striking and handsome plant, especially when in full flower. The very broad and rounded inflorescence easily separates this species from others in the genus. In our area restricted to the northeast quarter of New Mexico.

43. **Cryptantha osterhoutii** (Payson) Payson

*Oreocarya osterhoutii* Payson, Univ. Wyo. Publ. Bot. 1: 167. 1926. *C. osterhoutii* Payson, Ann. Mo. Bot. Gard. 14: 329. 1927. (*G. E. Osterhout 6138*, Monument Park, near Grand Junction, Mesa County, Colorado, 3 June 1921)

Densely caespitose perennials; *stems* slender, many arising from the densely branched multiple caudex, 0.7–1.2 dm tall, strigose and spreading setose; *leaves* spatulate to oblanceolate, obtuse, 1–3 cm long, 3–8 mm wide, dorsal surface strigose and appressed setose, pustulate, ventral surface strigose, the pustules mostly lacking; *inflorescence* open, 0.3–0.8 dm long, weakly white-setose; *bracts* inconspicuous; *calyx* in anthesis 2.5–4 mm long, in fruit becoming 5–6.5 mm long, the segments lanceolate, strigose and spreading setose; *corolla* white, the tube 2–3 mm long, crests at base of tube usually evident but poorly developed, fornices yellow, broad, emarginate, papillose, about 0.5 mm long, limb 5–7 mm wide; *style* exceeding mature fruit 0.2–0.7 mm; *nutlets* lanceolate, 2.7–3.2 mm long, 1.8–2.2 mm wide, usually less than four maturing, margins obtuse, not in contact, dorsal surface carinate, sharply tuberculate and rugose, ventral surface sharply tuberculate, scar open, constricted above the base, elevated margin evident but not conspicuous.

Sandy benches and rocky hillsides, 2,500–6,000 feet elevation. Southeastern Utah, and just into northeastern Arizona and Mesa County, Colorado. May to June.

A striking little plant that reaches its greatest concentration in the Canyonlands National Park area of southeastern Utah.

44. **Cryptantha insolita** (Macbr.) Payson

*Oreocarya insolita* Macbr. Contr. Gray Herb. 48: 28. 1916. *C. insolita* Payson, Ann. Mo. Bot. Gard. 14: 273. 1927. (*L. N. Goodding 2286*, Las Vegas, Clark County, Nevada, 4 May 1905)

Biennial or short-lived perennial from a slender taproot; *stems* 1–several, 3–4 dm tall, strigose and abundantly setose; *leaves* spatulate, mostly basal, obtuse, 3–5 cm long, 5–14 mm wide, dorsal surface subtomentose and sparsely appressed setose pustulate, ventral surface similar but the setae smaller and fewer, pustules few and inconspicuous, petioles long-hairy at the base; *inflorescence* open, 0.7–1.4 dm long, cymes few, much elongating, weakly setose; *bracts* inconspicuous; *calyx* in anthesis 3.5–4.5 mm long, in fruit becoming 7–9 mm long, the segments linear lanceolate, densely hirsute; *corolla* white, the tube 3–4 mm long, crests at base of tube well developed, fornices yellow, slightly emarginate, papillose, 0.5–1 mm long, limb 6–8 mm wide; *style* exceeding mature fruit 1–1.5 mm; *nutlets* ovate to lanceolate, 3.7–4 mm long, one to four maturing, the margins acute, in contact or nearly so, dorsal surface carinate, tuberculate, granulo-muricate and sometimes slightly rugose, ventral surface tuberculate and somewhat rugulose, scar narrow but open, the margin showing some tendency to become elevated.

Alkaline flats and rolling hills, 1,900–2,500 feet elevation. Known only from the region of Las Vegas, Nevada. April to June.

A rare endemic that may no longer exist because of the urbanization of the area of Las Vegas. The two known collections were labeled Las Vegas, so may have occurred in what is now the city or could possibly exist in outlying regions near the town.

45. **Cryptantha virginensis** (M. E. Jones) Payson

*Krynitzkia glomerata* var. *virginensis* M. E. Jones, Contr. W. Bot. 13: 5. 1910. *Oreocarya virginensis* Macbr. Proc. Amer. Acad. Arts 51: 547. 1916. *C. virginensis* Payson, Ann. Mo. Bot. Gard. 14: 274. 1927. (*M. E. Jones 5195a*, Laverkin, Washington County, Utah, 8 May 1894)

Biennial herbs; *stems* 1–several, from a stout taproot, 1.5–3(4) dm tall, setose-hirsute with spreading bristles; *leaves* oblanceolate to spatulate, obtuse, 3–10(12) cm long, 5–15 mm wide, dorsal surface sparsely setose, pustulate, also with some fine tangled pubescence beneath, ventral surface subtomentose and weakly appressed setose, with only a few pustulate hairs; *inflorescence* a broad thyrsus with the many individual cymes much elongating, 0.5–3 dm long; *bracts* conspicuous; *calyx* in anthesis 3–4 mm long, in fruit becoming 7–11 mm long, the segments linear-lanceolate, hirsute; *corolla* white, the tube 3–4 mm long, crests at base of tube conspicuous, fornices yellow, emarginate, papillose, about 1 mm long, limb 7–9 mm wide; *style* exceeding mature fruit 1–1.5 mm; *nutlets* ovate, 3.3–4.5 mm long, 2.4–2.6 mm broad, usually only one or two nutlets maturing, margins in contact, acute, dorsal surface with a distinct ridge, the surface tuberculate and usually rugulose, ventral surface very uneven with indeterminate rugae and tubercles, scar open and triangular, with an elevated margin.

Gravelly to clay soils mostly in the lower sonoran zone, 2,000–8,000 feet elevation. Southeastern California in Inyo and San Bernardino counties, eastward through southern Nevada into Washington County, Utah, and southward into Mohave and Coconino counties of Arizona. March to July.

Unlike most of the species of *Cryptantha*, this showy plant has very fragrant flowers.

### 46. **Cryptantha hoffmannii** I. M. Johnst.

*C. hoffmannii* I. M. Johnst. Contr. Arnold Arbor. 3: 90. 1932. *Oreocarya hoffmannii* Abrams, Ill. Fl. Pacif. States 3: 600. 1951. (*R. Hoffman 78*, rocky open slopes of Westguard Pass, Inyo County, California, 11 July 1930)

Biennial herbs; *stems* 1–several, 1.7–3(4) dm tall, conspicuously hirsute; *leaves* spatulate, crowded at the base, reduced upward, 2–5 cm long, 5–12 mm wide, spreading setose-hirsute, pustulate on both surfaces, but more so dorsally; *inflorescence* broad topped, interrupted, 1–2.8 dm long; *bracts* evident but not inconspicuous; *calyx* in anthesis 3–5 mm long, in fruit becoming 5–8 mm long, the segments lanceolate, hirsute-hispid; *corolla* white, the tube 3–4 mm long, crests at base of tube evident, fornices yellow, rounded, 0.5 mm long, papillose, limb 5–7 mm wide; *style* exceeding mature fruit 0.2–0.8 mm; *nutlets* ovate, 3–3.5 mm long, 2–2.5 mm wide, 2–4 nutlets maturing, the margins in contact, acute, both surfaces irregularly low rugose and minutely tuberculate, the dorsal with a low inconspicuous crest, scar open, triangular, with an elevated margin.

Gravelly soils in the *Pinyon-Juniper* association to the upper transition zone, 7,000–9,000 feet elevation. Southeastern California in Inyo County and just across the border into Nevada, mostly confined to the area of Westguard Pass. June to July.

### 48. **Cryptantha abata** I. M. Johnston

*Krynitzkia depressa* M. E. Jones, Contr. W. Bot. 13: 5. 1910. not *C. depressa* A. Nels. Bot. Gaz. 34: 29. 1902. *Oreocarya depressa* Macbr. Contr. Gray Herb. 48: 32. 1916. *C. modesta* Payson, Ann. Mo. Bot. Gard. 14: 278. 1927. not *C. modesta* Brand, Feddes Repert. Spec. Nov. Regni. Veg. 24: 48. 1924. *C. abata* I. M. Johnst. J. Arnold Arbor. 24: 240. 1928. (*M. E. Jones 6692*, Aurum, Nevada, 20 June 1893)

Long-lived perennial caespitose herbs; *stems* many, 0.5–1.8 dm tall, strigose and weakly setose; *leaves* oblanceolate to spatulate, obtuse, strigose, setose, and subtomentose, the petioles ciliate margined; *inflorescence* narrow, short, 0.2–0.8 dm long; *calyx* in anthesis 2.5–4 mm long, in fruit becoming 5–8 mm long, setose; *corolla* white, the tube 3–4 mm long, crests at base of tube conspicuous, fornices yellow, rounded, papillose, about 0.5 mm long, limb 7–8 mm wide; *style* exceeding mature fruit 0.5–1 mm; *nutlets* in contact, obtuse to acute, dorsal surface carinate, tuberculate, muricate and sometimes with low inconspicuous ridges, ventral surface deeply and irregularly rugose, scar open, triangular, surrounded by a slightly elevated margin.

Sandy to gravelly soils in the *Artemisia* and *Pinyon-Juniper* association, 4,000–9,000 feet elevation. Extreme eastern Nevada, south and western Utah, and Mohave County, Arizona. April to July.

*Cryptantha abata* is a tufted, often mat-forming plant. It is extremely rare in our flora but becomes very common at moderate elevations in Garfield and Piute counties, Utah.

### 49. **Cryptantha humilis** (A. Gray) Payson

*Eritrichium glomeratum* var. *humile* A. Gray, Proc. Amer. Acad. Arts 10: 61. 1875. *Oreocarya humilis* Payson, Ann. Mo. Bot. Gard. 14: 278. 1927. (*Bolander*, Summit Station, Donner Pass, Nevada County, California, 1871)

*C. nana* var. *ovina* Payson, Ann. Mo. Bot. Gard. 14: 314. 1927. *C. humilis* var. *ovina* Higgins, Brigham Young Univ. Sci. Bull. 13: no. 4. 37. 1971. (*G. H. Bentley*, vicinity of Currant, Nye County, Nevada, June 1916)

Short-lived perennial herbs; *stems* many, 0.5–3 dm tall, strigose to spreading setose-hirsute; *leaves* oblanceolate to spatulate, 1–6 cm long, 2–12 cm wide, strigose, setose, or subtomentose, pustulate on both surfaces; *inflorescence* narrowly cylindrical to open and lax, 0.2–1.8 cm long, tomentose to conspicuously setose; *bracts* inconspicuous; *calyx* in anthesis 2.5–4.5 mm long, in fruit becoming 6–13 mm long, setose or tomentose; *corolla* white, the tube 2.5–4.5 mm long, crests at base of tube conspicuous to nearly obsolete, fornices yellow, more or less papillose, rounded, about 0.5 mm long, limb 7–10 mm broad; *style* shorter than to exceeding mature fruit 2.5 mm; *nutlets* lanceolate to ovate-lanceolate, 3–4.5 mm long, 1.8–3.2 mm wide, 1 to 4 of them maturing, margins in contact, acute to obtuse, dorsal surface muricate, tuberculate, or somewhat rugulose, ventral surface indistinctly muricate or tuberculate, scar open, triangular, margin not elevated.

Mostly sandy or gravelly slopes, road cuts, and talus slopes of the higher mountains, 3,500–12,000 feet elevation. Sierra Nevada of California eastward to southeastern Oregon, southern Idaho to western Colorado and extreme northwestern Arizona. April to August.

*Cryptantha humilis* is a common member of the Great Basin flora, but enters our area only in southern Nevada and extreme northwestern Arizona. There are 5 varieties in the species complex, with only variety *ovina* (Payson) Higgins entering our area.

## 14. PLAGIOBOTHRYS F. & M.

Annual or perennial herbs; *stems* prostrate to erect, weak to somewhat robust, usually with slender appressed hairs, but at times setose though not pungently so; lower *leaves* opposite, alternate, or rosulate and crowded; *flowers* borne in slender racemes or spikes, occasionally glomerate, frequently bracted; *calyx* cleft to near the base, sometimes accrescent; *corolla* white, the tube short and included in the calyx, the fornices usually prominent and often yellow; *stamens* included, the filaments short; *nutlets* 4, or 1–3 by abortion, erect or incurved, roughened or rarely smooth, tending to be keeled on the back, and with a well-developed ventral keel extending from the tip to the middle or to the base, scar usually elevated and caruncle-like, mostly small, lateral to basal, placed at the base of the ventral keel; *gynobase* short and broad.

About 65 species native to western North America and South America with about 3 outlying species in Australia. (Name from the Greek, plagios, placed sideways, and bothros, pit or excavation, referring to the position of the nutlet scar.)

### References

Johnston, I. M. A synopsis and redefinition of the genus *plagiobothrys*. Contr. Gray Herb. 68: 57–80. 1923: and the Allocarya section of the genus *Plagiobothrys* in the western U. S. Contr. Arnold Arb. 3: 1–82. 1932.

Piper, C. V. A study of Allocarya. Contr. U.S. Nat. Herb. 79–113. 1920.

1. Leaves all alternate, scar lateral, near middle of nutlet ........ 2
— Leaves opposite at least below; scar lateral, oblique or basal ........ 9
2(1). Caruncle of nutlet elongate, extending along crest of the ventral keel; nutlets trigonous ........ 3
— Caruncle round or nearly so, at or below end of ventral keel ........ 4
3(2). Corolla 4–7 mm broad; nutlets irregularly rugose ........ 1. *P. kingii*
— Corolla 1–2.5 mm broad; nutlets conspicuously tessellate ........ 2. *P. jonesii*
4(2). Caruncle weakly developed, borne at tip of a short or conspicuous stipe; lowest leaves not in a rosette ........ 5
— Caruncle well developed, sessile on the nutlet; lowest leaves mostly in a rosette ........ 6
5(4). Stipe of nutlet elongate, about equalling the body in length; nutlets commonly united in pairs, plants of south and west Arizona ........ 3. *P. pringlei*
— Stipe of nutlet very short; nutlets distinct; plants mostly Californian ........ 4. *P. collinus*

6(4). Calyx circumscissle in fruit, less than 4 mm long; lobes usually connivent over fruit; nutlets usually only 1 or 2 .......... 7

— Calyx not circumscissle, or, if so, the strongly accrescent calyx over 4 mm long; calyx lobes erect or spreading; nutlets usually 4 .......... 8

7(6). Inflorescence a long, simple bracted raceme; nutlets highly incurved in lateral view, 1–2.5 mm long; corolla 2–3 mm broad .......... 5. *P. arizonicus*

— Inflorescence forked, bracted only at base if at all; nutlets low and flattened in lateral view 2–3 mm long; corolla 3–99 mm broad .......... . *P. nothofuluus*

8(6). Transverse dorsal crests of nutlets very narrow and sharp, enclosing polygonal granulate areolas .......... 7. *P. canescens*

— Transverse dorsal crests of nutlets very low and broad, separated only by low lineate ridges .......... 8. *P. tenellus*

9(1). Stems strigose or appressed hispidulous .......... 10

— Stems with distinctly spreading hairs; Mohave Desert of California .......... 12. *P. parishii*

10(9). Scar nearly basal; calyx lobes becoming elongate and thickened, tending all to be directed toward the same side of the fruit; plants mostly prostrate .......... 9. *P. leptocladus*

— Scar lateral or basilateral, calyx lobes neither elongate nor much thickened, symmetrically disposed; plants prostrate to ascending or erect .......... 11

11(10). Nutlets ovate to lanceolate; the evident scar mostly lateral but occasionally basilateral; plants west of continental divide .......... 10. *P. scouleri*

— Nutlets narrowly lanceolate to lance-linear, scar basilateral, small; plants east of the continental divide .......... 11. *P. scopulorum*

1. **Plagiobothrys kingii** (S. Wats.) A. Gray

*Eritrichium kingii* S. Wats. Bot. Kings Exp. 243. 1871. *Plagiobothrys kingii* A. Gray, Proc. Amer. Acad. Arts 20: 281. 1885. *Sonnea kingii* E. L. Greene, Pittonia 1: 23. 1887. (*S. Watson* 854, eastern side of the Sierra Nevada at Truckee Pass, California)

*Stems* erect, 1–several, 1–4 dm tall, hirsute, also villous-setose; *leaves* at base of plant narrowly oblanceolate, the cauline lance-linear, 2–6 cm long, hirsute to hispid, with spreading or ascending bristles; *inflorescence* cymose, the cymes dense in early flower, scorpioid, elongating in fruit and more laxly flowered; *bracts* evident at least on part of the inflorescence or flowers; *calyx* 5–6 mm long in fruit, the segments lanceolate, very hirsute-hispid; *corolla* 4–7 mm broad; *nutlets* 4, cuneate-ovoid, 2.5–3 mm long, acute and incurved at the apex, dorsal surface with a low median ridge and similar lateral keels on the edges, the whole irregularly rugose with broad papillate areolas; *scar* elongate, keel-like and medial.

Dry sandy to gravelly bajadas and valleys at 4,000–7,000 feet elevation. Southeastern Oregon, extreme eastern California, Nevada, and extreme western Utah. May to June.

Our plant is variety *kingii* and just enters the flora in southern Nevada. Variety *harknesii* (E. L. Greene) Jepson is a more northerly ranging form from northern Nevada and California into southeastern Oregon. The cymes on this phase are more congested and usually do not become as elongate.

2. **Plagiobothrys jonesii** A. Gray

*Plagiobothrys jonesii* A. Gray, Synop. Fl. N. Amer. 2: 430. 1886. *Sonnea jonesii* E. L. Greene, Pittonia 1: 23. 1887. (*M. E. Jones*, southeastern California on the Colorado near the Needles, 5 May 1884)

*Stems* erect, simple, widely branched with spreading or ascending branches, 1–3(4) dm tall, conspicuously hispid and villous-setose, the hairs pustulate; *leaves* oblanceolate to linear at the base 2–6 cm long, the cauline lanceolate, conspicuously spreading hirsute, the hairs with pustulate bases; *inflorescence* congested when immature, the scorpioid cymes only slightly elongating at maturity 1.5–4(7) cm long, some of the lower leaves also with axillary flowers; *bracts* lacking; *calyx* 6–10 mm long in fruit, the segments linear-subulate, spreading hirsute; *corolla* 1–2 mm broad; *nutlets* 2 or 3, incurved, 4 angled by the dorsal and ventral keels and the lateral ridges, 2.5–3.5 mm long, apex acute, the keel and lateral angles tuberculate, the surface between tessellate; *scar* narrow, merging into the keel above and with a diverging lateral ridge extending to either side.

Gravelly wash bottoms, rocky ridges, and desert bajadas below 5,800 feet elevation. Southern California eastward to southern Nevada, southwestern Utah, and western Arizona, south into Sonora, Mexico. March to May.

*Plagiobothrys jonesii* differs from all other members of the genus in that it resembles a *Cryptantha* in habit and an *Amsinckia* in nutlet characteristics.

3. **Plagiobothrys pringlei** E. L. Greene

*Echidiocarya arizonica* A. Gray in Bentham & Hooker's Gen. Pl. 2: 854. 1876; Proc. Amer. Acad. Arts 11: 89. 1876. non *P. arizonicus* (A. Gray) Greene. *Plagiobothrys pringlei* E. L. Greene, Pittonia 1: 21. 1887. (*Dr. Smart*, Verde Mesa, Arizona)

*Stems* several to many, branched from near the base, prostrate or decumbent to nearly erect, slender, 1–4 dm long, spreading setose with fine short hairs; *leaves* numerous below, gradually reduced above, narrowly oblanceolate to linear, 2–4(6) cm long, 2–5 mm broad, obtuse to acute at apex, appressed strigose or canescent to conspicuously setose; *inflorescence* an elongate spike, floriferous to near the base of the stem; *bracts* conspicuous, 1–2 cm long; *calyx* 3–4.5 mm long in fruit, the segments linear-lanceolate, canescent; *corolla* 2–3 mm broad, inconspicuous; *nutlets* 4, those near the base of stem commonly joined in pairs, the upper separate, ovate, acute at apex, 1.8–2 mm long, dorsal keel evident near the apex but fading to distinct tuberculations below, the surface also rugulose with short ridges; *scar* elevated on a prominent stipe at least 1.3 mm long, and usually as long as the nutlet.

On sandy or gravelly desert flats and bajadas. Common in Cochise, Maricopa, Pima, and Pinal counties of Arizona, and northern Sonora, Mexico. March to April.

4. **Plagiobothrys collinus** (Ph.) I. M. Johnston

*Plagiobothrys californicus* var. *fulvescens* I. M. Johnst. Contr. Gray Herb. 68: 74. 1923. *Allocaryastrum ursinum* var. *fulvescens* Brand, Pflanzenr. IV 252: 101. 1931. *Echidiocarya californica* subsp. *fulvescens* L. Abrams. Ill. Fl. Pacific States 3: 571. 1951. *P. collinus* var. *fulvescens* Higgins Great Basin Nat. 34(2):165. 1974. (*T. S. Brandegee*, Santa Barbara, California, 1881)

*P. micranthus* A. Nels. Amer. J. Bot. 25: 115. 1938. (A. *Nelson 10232*, Prescott, Arizona, moist creek banks, 28 April 1925)

*Stems* slender, elongate, prostrate or decumbent, 1–4 dm long, hispidulous; *leaves* oblanceolate, obtusish to acutish, 1–3 cm long, 3–5 mm broad, hirsute; *inflorescence* an elongate spike, remotely flowered and very slender; *bracts* lacking above the middle of inflorescence; *calyx* 2.8–3.2 mm long in fruit, the segments linear-lanceolate, hispidulous; *corolla* 2–2.5 mm broad; *nutlets* 4, ovoid, 1.5 mm long, dorsal keel thin above, reduced to a mere line and fading out about middle of nutlet, irregularly rugose, also muriculate; *scar* on a short stipe near base of nutlet.

Dry, open flats, mesas, and valleys, ascending to moderate elevations in the foothills. Southern California, northern Baja California, Mexico, eastward to westward Arizona and Sonora, Mexico, and in Chile of South America. February to May.

*P. collinus* is divided into five rather distinct varieties in western North and South America. The only phase that enters our area is variety *fulvescens*, with its elongate laxly flowered spikes and harsher, more penetrating pubescence.

5. **Plagiobothrys arizonicus** (A. Gray) E. L. Greene

*Eritrichium canescens* var. *arizonicum* A. Gray. Proc. Amer. Acad. Arts 17: 227. 1882. *Plagiobothrys arizonicus* E. L. Greene ex A. Gray, Proc. Amer. Acad. Arts 20: 284. 1885. (*C. G. Pringle 364*, near Camp Lowell, Arizona, 9 April 1881)

*Stems* loosely ascending to erect, usually branched below the middle, 1–4(5) dm tall, hirsute-hispid, also somewhat villous, the basal part of the stem and the root highly charged with a purple dye; *leaves* linear-oblanceolate, 1.5–5(6) cm long, 2–6(10) mm broad, hirsute, with pustulate hairs, the midvein and its branches strong dye stained; *inflorescence* spikelike, elongate, and remotely flowered, 3–15 cm long; *bracts* mostly lacking on all flowers but with several scattered along the spikes; *calyx* 3–3.5 mm long in fruit, lobed to about the middle, circumscissle, the segments connivent and narrowly lanceolate, hirsute and somewhat villous; *corolla* 2–2.5 mm broad; *nutlets* 1–4, commonly

2, ovoid, abruptly acute at apex, the dorsal surface with rectangular smooth areolae marked off by narrow tuberculate ridges and rugae; *scar* median in a sunken area at base of keel.

Dry desert slopes and mesas, often near the base of rocky outcrops, extending to moderate elevations in the mountains 7,000 feet. Western edge of the San Joaquin Valley, California, eastward through southern Nevada to southern Utah, New Mexico, and south into Sonora, Mexico. March to May.

6. **Plagiobothrys nothofulvus** (A. Gray) A. Gray

*Eritrichium nothofulvum* A. Gray, Proc. Amer. Acad. Arts 17: 227. 1882. *Plagiobothrys nothofulvus* A. Gray, Proc. Amer. Acad. Arts 20: 285. 1885. (*Douglas*, California)

*Stems* 1–several, simple or more often ascendingly branched from the base, 1.5–5(6) dm tall, villous-hispidulous with spreading hairs, base of plant often slightly dye stained; *leaves* at base oblanceolate 3–10 cm long, 5–20 mm broad, acute at apex, sparsely villous-setose, cauline leaves few, linear-lanceolate to lanceolate; *inflorescence* elongate, loosely flowered, racemes often paired, 5–15(20) cm long; *bracts* lacking; *calyx* 2–3 mm long in fruit, lobed to about the middle, circumscissle, the segments narrowly lanceolate, fulvous-hirsute; *corolla* 6–9 mm broad, showy; *nutlets* 1 to 4, 2–3 mm long, round-ovoid, abruptly constricted to an acute apex, loosely rugulose-reticulate and somewhat granular tuberculate; *scar* annular, median at the base of the narrow ventral keel.

Open grassy slopes, fields, and roadsides, mostly below 2,500 feet elevation. Southern Washington along the Columbia River, south through Oregon and California on the west slope of the Sierra Nevadas to the Coastal Ranges to northern Baja California, Mexico, occasionally at the desert edge in eastern Kern County, California. March to May.

*Plagiobothrys nothofulvus* just enters our flora along the extreme western boundary in California.

7. **Plagiobothrys canescens** Benth.

*Plagiobothrys canescens* Benth. pl. Hartweg. 326. 1849. *Eritrichium canescens* A. Gray, Proc. Amer. Acad. Arts 10: 57. 1874. (*Hartweg*, Sacramento Valley, California)

*P. microcarpa* E. L. Greene, Pittonia 1: 21. 1887. (*Mrs. R. M. Austin*, Butte County, California, May 1883)

*P. canescens* var. *apertus* E. L. Greene, Pittonia 1: 21. 1887. (*E.L. Greene*, plains of the upper San Joaquin, 1884)

*Stems* many, branched from the base, decumbent or prostrate, rarely erect, 1–4(6) dm long, villous or finely hispidulous; *leaves* linear to linear-oblanceolate, 1.5–5 cm long, 2–7 mm broad, the cauline well developed; *inflorescence* elongate and loosely flowered in age, 5–25 cm long; *bracts* conspicuous and well developed, 1–2 cm long; *calyx* in fruit 4–6 mm long, the segments lanceolate, densely rufous-villous-tomentose; *corolla* 2.7–3.5 mm broad; *nutlets* mostly 4, round-ovoid, abruptly constricted to the narrow acute apex, strongly incurved, obscurely tuberculate, but with conspicuous transverse rugae forming rectangular papillate intervals; *scar* median, annular, slightly raised.

Gravelly to clayey slopes, plains, and grassy hillsides, also alkaline flats, mostly below 4,500 feet elevation. Nearly throughout the length of California, mostly west of the Sierra Nevada, entering the Mohave Desert in Inyo, Kern, and San Bernardino counties. March to May.

8. **Plagiobothrys tenellus** (Nutt.) A. Gray

*Myosotis tenella* Nutt. ex Hook. J. Bot. Kew Gard. Misc. 3: 295. 1851. *Eritrichium tenellum* A. Gray, Proc. Amer. Acad. Arts 10: 57. 1874. (*Geyer*, "mountains along the Coeur d'aleine River," Idaho)

*Stems* 1–several, slender, erect or ascending, 1–3 dm tall, soft-villous; *leaves* mostly basal, rosettelike, lance-oblong to lance-elliptic, 1–4 cm long, 2–8 mm broad, sessile, cauline leaves few, ovate to lanceolate, shorter than the basal ones; *inflorescence* open, loosely flowered, tending to elongate in age, slender, 4–15 cm long; *bracts* evident only near the base; *calyx* in fruit 3–5 mm long, the segments ovate-lanceolate, short villous, whitish or fulvous; *corolla* 2–3 mm broad; *nutlets* usually 4, 1.5–2.5 mm long, thick cruciform, usually light colored, sharply ridged dorsally and on the edges, tuberculate on the ridges, smooth and shiny between the ridges; *scar* small, set just below middle of nutlet at end of keel.

Grassy, sandy, or gravelly slopes, hillsides, and dry open areas below 5,000 feet elevation. Common from California to British Columbia and Idaho, becoming rather rare in Utah and Nevada, and with several highly scattered locations in Graham, Gila, Maricopa, Pinal, and Pima counties of Arizona. March to June.

9. **Plagiobothrys leptocladus** (E. L. Greene) I. M. Johnston

*Eritrichium californicum* var. *subglochidiatum* A. Gray, Bot. Calif. 1: 526. 1876. *Krynitzkia california* var. *subglochidiata* A. Gray, Proc. Amer. Acad. Arts 20: 266. 1885. *Allocarya californica* var. *subglochidiata* Jepson, Fl. W. Middle Calif. 443. 1901. *Allocarya subglochidiata* Piper, Contr. U. S. Natl. Herb. 11: 485. 1906. (S. *Watson 851*, Clover Mountains, Elko County, Nevada, Lectotype by Johnston)

*Allocarya leptoclada* E. L. Greene, Pittonia 3: 109. 1896. *Plagiobothrys leptocladus* I. M. Johnst. Contr. Arnold Arbor. 3: 38. 1932. (*E. L. Greene*, Pine Creek, Eureka County, Nevada, 20 July 1896)

*Stems* prostrate, 1–3(7) dm long, somewhat succulent, sparsely strigose to subglabrous; *leaves* linear or linear-oblanceolate, 3–8 cm long, 2–5 mm broad, 1 or more pair near the base opposite, dorsal surface sparsely strigose-pustulate, subglabrous above; *inflorescence* spikelike, elongate, loosely flowered to near base of plant, the spikes somewhat unilateral; *bracts* evident at least below; *calyx* very accrescent, in fruit becoming 4–8 mm long, the segments linear, slightly thickened and succulent, all tending to be directed toward the same side of the fruit; *corolla* minute, 1–2 mm broad; *nutlets* 1–4, lanceolate, 1.5–2.5 mm long, dorsal surface rugose-tuberculate, granulate, or penicillate-hairy, ventral surface angulate, keeled the entire length; *scar* basal or nearly so, not surrounded by a ridge.

Moist depressions of clay flats, usually in alkaline soils. Oregon south to northern Baja California, Mexico, eastward to western Wyoming and northern Utah, entering the desert edge in Kern and San Bernardino counties of California. April to July.

In northern Utah *P. leptocladus* often forms prostrate mats a meter or more in diameter from a single plant, but this is relatively rare throughout most of its range.

10. **Plagiobothrys scouleri** (H. & A.) I. M. Johnston

*Allocarya cusickii* E. L. Greene, Pittonia 1. 17. 1887. *Plagiobothrys cusickii* I. M. Johnst. Contr. Arnold Arbor. 3: 63. 1932. (W. C. *Cusick*, Union County, Oregon, in 1883) = var. *cusickii*

A. *hispidula* E. L. Greene, Pittonia 1: 17. 1887. *Plagiobothrys hispidulus* I. M. Johnst. Contr. Arnold Arbor 3: 71. 1932. (S. *B. Parish 1470*, Bear Lake, San Bernardino Mountains, California) = var. *penicillatus*

A. *penicillata* E. L. Greene, Pittonia 1: 18. 1887. A. *hispidula* var. *penicillata* Jepson, Man. Fl. Pl. Calif. 853. 1925. (*E. L. Greene*, Donner Lake in the Sierra Nevada, California, August 1883)

A. *cognata*, E. L. Greene, Pittonia 4: 235. 1901. *Plagiobothrys cognatus* I. M. Johnston. Contr. Arnold Arbor 3: 59. 1932. (*Mulford 147*, in part, Cache Valley, Utah, 17 June 1898) = var. *penicillatus*

*Stems* prostrate or ascending, several to many, 2–1.5 dm long, strigose; *leaves* essentially all cauline, linear, 1.5–6.5 cm long, 2–5 mm broad, the lowermost opposite, the others alternate, sparsely to densely strigose; *inflorescence* and elongate, loosely flowered raceme or spike that is floriferous to near base of plant; *bracts* evident at least below; *calyx* 2–3.5 mm long in fruit, the segments linear-lanceolate, hispidulose; *corolla* inconspicuous, 2–4 mm broad; *nutlets* usually 4, ovate, to lance-ovate, 1.5–2 mm long, rugose and tuberculate to nearly smooth, with or without penicillate bristles; *scar* small lateral to basilateral.

Moist areas along roadsides, open mountain meadow depressions and along slow-moving stream banks, 4,000–10,500 feet elevation. Alaska, south through British Columbia and Saskatchewan, to California, Arizona, and New Mexico. May to August.

*P. scouleri* is a highly variable and complex species, probably due to the fact that many incipitent species are in the process of being evolved. The species and its varieties are centered somewhat to the northwest of our flora; however two varieties, which are separated by the following key, enter our area.

1. Nutlets smooth, glossy; stems and leaves sparsely strigose to glabrous; southern Nevada in Clark County in our flora .............................. var. *cusickii* (Greene) Higgins

— Nutlets rugulose or tuberculate, dull, often penicillate bristly; stems and leaves abundantly strigose or hispidulous, Arizona and New Mexico in our flora .......... ........................................................................................ var. *penicillatus* (Greene) Cronquist

11. **Plagiobothrys scopulorum** (E. L. Greene) I. M. Johnston

*Allocarya scopulorum* E. L. Greene, Pittonia 1: 16. 1887. *Plagiobothrys scopulorum* I. M. Johnst. Contr. Gray Herb 68: 79. 1923. (*E. L. Greene*, Denver, Colorado, 15 June 1870)

*Stems* mostly ascending but occasionally prostrate, 5–25 cm tall, branched from near the base, strigose; *leaves* linear, strigose, 1–5 cm long, 1–4 mm broad; *inflorescence* loosely flowered, floriferous to near base of plant; *bracts* evident, mostly near the base; *calyx* 2.5–3.5 mm long in fruit, the segments lance-linear, not accrescent, strigose-hispidulous; *corolla* inconspicuous, 1–2 mm broad; *nutlets* 4, 1.5–2 mm long, lanceolate, rugulose and tuberculate, the ridges rather inconspicuous; *scar* basilateral to nearly basal, small.

Moist areas at roadsides and depressions in the prairie sod to moderate elevations in the mountains. Mostly east of the Continental Divide from Saskatchewan south through much of the northern prairie to Nebraska, the Dakotas, and northern New Mexico. July to September.

The fruit of *P. scopulorum* is very similar to that of *P. leptocladus*, but the habit, indument, and calyx are entirely different, and more like that of *P. scouleri*. These differences correlated with geography distinguished this plant as being at least somewhat different.

12. **Plagiobothrys parishii** I. M. Johnston

*Eritrichium cooperi* A. Gray, Proc. Amer. Acad. Arts 19: 89. 1883. *Krynitzkia cooperi* A. Gray, Proc. Amer. Acad. Arts 20: 267. 1885. *Allocarya cooperi* E. L. Greene, Pittonia 1: 19. 1887. non *P. cooperi* A. Gray. *Plagiobothrys parishii* I. M. Johnst. Contr. Gray Herb. 68: 78. 1923. (*Dr. Cooper*, Mohave Desert, southeastern California, at Camp Cady, 1860–61)

*Stems* diffusely branched from near the base, erect or ascending, 0.5–3 dm tall, hirsute with short, stout, spreading bristles; *leaves* linear or the upper oblong, hispidulous and with pustules on the dorsal surface, 1–5 cm long, 2–4 mm wide; *inflorescence* in age becoming loose and slender, 3–10 cm long; *bracts* few, near the base; *calyx* 2–3 mm long in fruit, early deciduous, the segments oblong to lanceolate, hispidulous; *corolla* 3–5(6) mm broad, white with a yellow throat; *nutlets* ovate to lance-ovoid, more or less slightly heteromorphic with the axil nutlet slightly larger, plumper, and with a triangular-ovate scar, the others with a sublinear scar, apex on both nutlets acute, dorsal surface keeled at apex only, strongly rugose with transverse ridges.

Wet alkaline soil around desert springs, 2,500–4,500 feet elevation. Southeastern California in Inyo, Mono, and San Bernardino counties. April to June.

*Plagiobothrys parishii* is a rather narrow endemic of the Mohave Desert, having been collected in a few scattered stations, but is quite common about Rabbit Springs in San Bernardino County.

## 15. MERTENSIA Roth.

Plants perennial herbs from fleshy fusiform, rhizomelike or cormlike roots; *stems* erect or ascending, glabrous to somewhat pubescent 3–17 dm tall, unbranched below the inflorescence; *leaves* entire, linear to cordate, sessile or petiolate, alternate; *inflorescence* lax or congested, ebracteate, unilateral, modified scorpioid cyme, or becoming panicled in age; *calyx* 5-parted, occasionally campanulate, often accrescent; *corolla* tubular, campanulate, with or rarely without fornices in the throat, blue, occasionally white or pink; *filaments* attached below the throat; *anthers* exserted or included; *style* shorter or longer than the corolla; *ovary* 2 celled; *nutlets* 4, or by abortion fewer, attached laterally to the gynobase at or below the middle, generally rugose.

A genus of about 35 species of Eurasia and North America, mainly in the western half. (Named for F. C. Mertens, 1764–1831, German botanist.)

### References

Johnston, I. M. Studies in the Boraginaceae, IX. 2. Notes on various borages of the western United States. Contr. Arnold Arb. 3: 83–98. 1932.

Macbride, J. F. The True Mertensias of western North America. Contr. Gray Herb. n.s. 48: 1–20. 1916.

Williams, L. O. A Monograph of the Genus *Mertensia* in North America. Ann. Mo. Bot. Gard. 24: 17–159. 1937.

1. Plants relatively tall and robust (4–15 dm tall when fully developed), with evident lateral veins in the cauline leaves; flowering in late spring and summer ...... 2

— Plants smaller, seldom as much as 4 dm tall, usually without evident lateral veins in the cauline leaves; blooming as soon as snow and temperature permit .. .......... 3

2(1). Leaves strigillose on the upper surface; calyx-lobes acute ................ 1. *M. franciscana*

— Leaves glabrous or somewhat papillose above, not hairy; calyx-lobes rather obtuse, ciliate on the margins .......... 2. *M. ciliata*

3(1). Filaments narrower and much shorter than the anthers, the base of the anthers not elevated beyond the fornices; alpine plants .......... 3. *M. alpina*

— Filaments longer and more conspicuous, broad and flattened; base of anthers elevated well above the fornices; plants alpine or not .......... 4

4(3). Nutlets without an elevated margin or border; plants not of Arizona .......... 4. *M. lanceolata*

— Nutlets with the margin elevated, forming a definite border; plants of northern Arizona .......... 5. *M. macdougalii*

1. **Mertensia franciscana** A. A. Heller

*Mertensia franciscana* A. A. Heller, Bull. Torrey Club 26: 549. 1899. (*D. T. Macdougal* 232, vicinity of Flagstaff, 7,000 feet, 15 July 1898)

*M. pratensis* A. A. Heller Ibid. 550. 1899. (*Heller* & *Heller 3641*, Santa Fe Canyon, 9 miles east of Santa Fe, 2 June 1897)

*M. alba* Rydb. Bull. Torrey Club 31: 638. 1904. *M. pratensis* f. *alba* J. F. Macbride, Contr. Gray Herb. 48: 8. 1916. (*Baker, Earle,* & *Tracy* 825, La Plata River, 10,500 feet, 13 July 1898)

*M. grandis* Woot. & Standl. Contr. U. S. Natl. Herb. 16: 165. 1913. (*O. B. Metcalfe 1319*, south end of the Black Range, Hillsboro Peak, Grant County, New Mexico, 11 September 1904)

*Stems* erect or ascending (1)3–10 dm tall, glabrous; *leaves* at base oblong-elliptic to elliptic 6–20 cm long, 1–3.5(4.5) cm broad, base acute-attenuate to subcordate, apex acuminate to acute, upper surface, very short strigillose, lower surface glabrous; *petioles* longer or shorter than the blade, cauline leaves elliptic to lance-ovate, 4–14 cm long, 1–3(6) cm broad, becoming sessile toward the inflorescence; *inflorescence* paniculate; *bracts* lacking; *calyx* 2.5–5 mm long, the segments linear to lanceolate, acute, divided nearly to the base, glabrous or pubescent on the back, conspicuously ciliate on the margins; *pedicels* 1–20 mm long, strigose; *corolla* tube 5–9 mm long, glabrous or pubescent within, limb 4–9 mm broad, moderately expanded, fornices, prominent, usually pubescent; *anthers* 2.5–3 mm long, longer than the filaments; *style* 9–20 mm long; *nutlets* rugose and papillate.

Stream banks, moist meadows, and openings in pine forests, 6,000–11,000 feet elevation. Eastern Nevada and Arizona, eastward to Colorado and New Mexico. June to August.

This is by far the most common bluebell in our area, it is very common throughout the mountainous areas of New Mexico and Arizona.

2. **Mertensia ciliata** (Torr.) G. Don

*Pulmonaria ciliata* Torr. Annals Lyceum N. Y. 2: 224. 1827. *Mertensia ciliata* G. Don, Gen. Syst. 4: 372. 1837. (*James*, Rocky Mountains of Colorado)

*Mertensia picta* Rydb. Bull. Torrey Club 31: 638. 1904. (*G. E. Osterhout* 2833, Estes Park, Larimer County, Colorado, 20 July 1903)

*Stems* many from the branched caudex, 1.5–15 dm tall, glabrous; *leaves* variable, at the base of the plant oblong to ovate or lance-subcordate, 4–15 cm long, 2–6(10) cm broad, ciliate on the margins, glabrous or papillate on the surfaces, petioles longer or shorter than the blades, cauline leaves lanceolate to ovate, acute, acuminate or obtuse at apex, attenuate to subcordate at base, mostly sessile; *inflorescence* paniculate; *bracts* lacking; *calyx* 1.5–3 mm long, the segments oblong to nearly lanceolate, obtuse or rounded at the apex, not accrescent, glabrous on the back, the margins ciliate; *pedicels* 1–10 mm long, glabrous or with a few strigose hairs; *corolla* tube 4–6(8) mm long, the limb 4–10(15) mm broad, moderately expanded, fornices evident, glabrous to pubescent; *anthers* 1–2.5 mm long, as long as or shorter and narrower than the expanded part of the filaments; *style* about as long as corolla or exceeding it; *nutlets* rugose or papillate. N = 12, 24.

Stream banks, wet meadows, and moist hillsides up to 12,000 feet elevation. Mountains of Montana and eastern Oregon, southeastward to Utah, Wyoming, Colorado, and northern New Mexico. July to September.

*Mertensia ciliata* resembles *M. franciscana* in general aspect but is easily separated from the latter by its glabrous leaves and stems and the small obtuse calyx segments. This plant only enters our flora in the higher elevations in northern New Mexico.

3. **Mertensia alpina** (Torr.) G. Don

*Pulmonaria alpina* Torr. Annals Lyceum N. Y. 2: 224. 1828. *Mertensia alpina* G. Don, Gen. Hist. 4: 372. 1838. *Cerinthodes alpinum* Kuntze, Rev. Gen. Pl. 2: 436. 1891. (*James*, Rocky Mountains)

*Mertensia obtusiloba* Rydb. Bull. Torrey Club 28: 32. 1901. *M. brevistyla* var. *obtusiloba* A. Nels. Man. Rocky Mt. Bot. 421. 1909. (*F. Clements*, Pikes Peak, Colorado, 1900)

*Stems* 1–numerous, glabrous, erect or ascending, 0.5–2(3) dm tall; *leaves* at base of plant linear-lanceolate to oblong or elliptic, 1–5(7) cm long, 0.7–1.5(2) cm broad, strigose above, glabrous beneath, the winged petiole shorter than the blade, cauline leaves lanceolate to elliptic, sessile, 1–6 cm long, 0.3–1.8 cm broad; *inflorescence* compact, or slightly panicled in age; *bracts* lacking; *calyx* 2–3(5) mm long in fruit, divided to near the base, the segments linear-lanceolate to oblong, obtuse to acute at the apex, ciliate; *pedicels* 1–10 mm long, strigose to glabrous; *corolla* tube 3–6(11) mm long, glabrous within, limb widely spreading (5)7–10(11) mm wide; *fornices* prominent, nearly closing the throat; *anthers* about 1–1.3 mm long, usually longer than the filaments, inserted in the tube and not projecting beyond it; *style* short, about equalling the calyx; *nutlets* rugose, about 2 mm long.

Above timberline, in the high mountains on open dry meadows and slopes. Southwestern Montana and adjacent Idaho, south to Colorado and northern New Mexico. July and August.

4. **Mertensia lanceolata** (Pursh) A. DC.

*Pulmonaria lanceolata* Pursh. Fl. Amer. Sept. 2: 729. 1814. *Casselia lanceolata* Dumort. Com. Bot. 24. 1822. *Cerinthodes lanceolatum* Kuntze, Rev. Gen. Pl. 2: 436. 1891. (*Bradbury*, in upper Louisiana, 18 June 1811)

*P. marginata* Nutt. Gen. 1: 115. 1818. *Lithospermum marginatum* Spreng, Syst. 1: 547. 1825. *Mertensia marginata* G. Don, Gen. Hist. 4: 319. 1838. (*Nuttall*, Missouri)

*Mertensia fendleri* A. Gray, Amer. J. Arts Sci. 34: 339. 1862. *Mertensia lanceolata* var. *fendleri* A. Gray, Proc. Amer. Acad. Arts 10: 53. 1875. (*Fendler 625*, Santa Fe creek bottom, 1847)

*Mertensia viridis* A. Nels. Bull. Torrey Club 26: 244. 1899. *Mertensia lanceolata* var. *viridis* A. Nels. First Report Fl. Wyoming 158. 1896. (*A. Nelson 1608*, Laramie Peak, 6 August 1895)

*M. bakeri* E. L. Greene, Pittonia 4: 90. 1899. (*Baker, Earle, & Tracy 576*, Hayden Peak, Colorado, 13,000 feet, 14 July 1898)

*M. cynoglossoides* E. L. Greene, Pl. Baker. 3: 19. 1901. *M. viridis* var. *cynoglossoides* Macbr. Contr. Gray Herb. 48: 13. 1916. (*Baker 191*, Black Canyon, Colorado, 20 June 1901)

*M. caelestina* Nels. & Ckll. Proc. Biol. Soc. Wash. 16: 46. 1903. *M. viridis* var. *caelestina* Williams, Ann. Mo. Bot. Gard. 24: 114. 1937. (*Cockrell 40*, Truchas Peak, New Mexico, in 1902)

*M. amplifolia* Woot. & Standl. Contr. U. S. Natl. Herb. 16: 165. 1913. (*Vasey*, Glorietta, New Mexico, June 1881)

*M. fendleri* var. *pubens* Macbr. Contr. Gray Herb. 48: 14. 1916. *M. lanceolata* var. *pubens* Williams, Ann. Mo. Bot. Gard. 24: 98. 1937. (*Standley 4023*, Winsor's Ranch, along the Pecos River, 29 June 1908)

*Stems* 1–many, 1–4.5 dm tall, erect or ascending, canescent to glabrous; *leaves* at base of plant ovate to elliptic or oblanceolate, 1.5–14 cm long, 0.3–3.5 cm broad, glabrous to densely canescent on both surfaces, sessile or with the petioles longer than the blade, cauline leaves only moderately reduced toward the inflorescence, mostly sessile; *inflorescence* congested to loosely paniculate, especially in age; *bracts* only near the base; *calyx* 2–5(8) mm long in fruit, divided to below the middle and mostly to near the base, the segments lanceolate to ovate-triangular, glabrous to strigose; *pedicels* 1–15 mm long, strigose to glabrous; *corolla* tube 3–7 mm long, with a ring of dense hairs near the base, the limb 3–9 mm broad, moderately expanded; *fornices* conspicuous, glabrous to pubescent; *anthers* 1–2 mm long, well exserted from the tube; *style* shorter or longer than the corolla tube; *nutlets* 2–3 mm long, rugose.

Moderately moist to dry open slopes and ridges in the mountains, 6,000–11,000 feet elevation. Saskatchewan, Montana, and North Dakota, south through Colorado, Utah, and Wyoming into northern New Mexico.

June to September.

*Mertensia lanceolata* is a poorly defined species. *Mertensia bakeri* and *M. viridis* seem to be only ecotypes of the larger, more wide-ranging *M. lanceolata*. There are no clearly defined morphological differences that can be correlated with geography to aid in the separation of species. There may be enough variation in this heterogeneous mixture, here called *lanceolata* to warrant a variety or two, but none are here proposed.

5. **Mertensia macdougalii** A. A. Heller

*Mertensia macdougalli* A. A. Heller, Bull. Torrey Club 26: 550. 1899. (*MacDougal* 95, near Mormon Lake, south of Flagstaff, Arizona, 12 June 1898)

*Stems* ascending, 1–several, 0.8–2.5 dm tall, glabrous; *leaves* at base oblong-oval to obovate, petiolate, 2–5 cm long, 1–2.8(4) cm broad, glabrous, pustulate, the cauline leaves, sessile, oblong-lanceolate to ovate, 2–4 cm long, 0.5–2 cm broad; *inflorescence* a modified dense scorpioid cyme, not much elongating in age; *bracts* lacking; *calyx* in anthesis 5–6 mm long, in fruit becoming 7–10 mm long, divided to below the middle, the segments lance-oblong, ciliate; *pedicels* 1–10 mm long, glabrous; *corolla* tube 8–9 mm long, glabrous within, the limb 5–6 mm broad, moderately expanded; *fornices* conspicuous, glabrous; anthers 2.5–3 mm long, subequal to the filaments; *style* usually exceeding the corolla; *nutlets* rugose, inner surface slightly concave, the margin forming a collar.

Moist rich soil at medium elevations, 6,000–9,000 feet. Coconino and Yavapai counties, Arizona.

## 16. ERITRICHIUM Schrad.

Depressed-pulvinate perennial plants; *stems* 2–10 cm tall, or sometimes acaulescent; *leaves* small, usually densely hairy, crowded on the numerous short shoots or a base of the elongate stem; *inflorescence* a false raceme or spike terminating the short stem, naked or leafy bracteate; *pedicels* erect; *calyx* cleft nearly to the base; *corolla* blue, rarely white, often with a yellow eye, salverform, with a short, narrow tube; *fornices* well developed; *filaments* attached well down in the corolla tube; *anthers* included; *ovary* 4 lobed; *stigma* 1; *nutlets* 1–4, smooth, attached basilaterally to the low stout gynobase, the apex obliquely truncate, this portion surrounded by an entire or toothed margin.

A genus of about 4 species of Eurasia and western North America. (From the Greek erion, wool and trichos, hair, referring to the wooly pubescence of *E. nanum*, the original species.)

### Reference

Wight, William R. The genus *Eritrichium* in North America. Bull. Torrey Club 29: 407–14. 1902.

1. **Eritrichium nanum** (Vill.) Schrad.

*Myosotis nana* Vill. Prosp. 21. 1779. *Eritrichium nanum* Schrad. Asperif. 16. 1820. *Omphalodes nana* A. Gray, Proc. Amer. Acad. Arts 20: 263. 1885. *Lappula nana* Car. in Parl. & Car. Fl. Ital. 6: 861. 1886. (Presumably from the Alps)

*Eritrichium aretioides* var. *elongatum* Rydb. Mem. N.Y. Bot. Gard. 1: 327. 1900. *E. elongatum* Wight, Bull. Torrey Club. 29: 408. 1902. *E. nanum* var. *elongatum* Cronq. Vasc. Pl. Pacif. N. W. 4: 203. 1959. (*Rydberg* & *Bessey* *4891*, Spanish Basin, Montana, 26 June 897) = var. *elongatum*.

*Eritrichium argenteum* Wight, Bull. Torrey Club. 29: 411. 1902. *E. elongatum* var. *argenteum* I. M. Johnst. Contr. Gray Herb. 70: 53. 1924. *E. nanum* ssp. *villosum* var. *villosum* f. *argenteum* Brand, Pflanzenr. IV 252 (Heft. 97): 191. 1931. (*Crandall* & *Cowan* *361*, northwest of Como, Colorado, 31 July 1895) = var. *elongatum*.

Pulvinate-caespitose, long-lived perennials; *stems* acaulescent or caulescent with short, slender, erect stems, 0.1–0.7(1) dm tall, villous to densely strigose; *leaves* oblanceolate to oblong or narrowly ovate, 5–10 mm long, 1–2(3) mm broad, villous to loosely strigose; *inflorescence* compact when sessile among the leaves or racemelike when borne on a leafy flowering branch, capitate; *calyx* 1.8–2.3 mm long in fruit, linear, villous or silky strigose; *corolla* tube short, 2–2.5 mm long, yellowish, the limb blue rarely white 4–8 mm broad; *fornices* prominent, papillose; *nutlets* 1–4, glabrous, somewhat asymmetrical, margined, with an entire or toothed margin.

Open rocky slopes, dry meadows, and on tundra at high elevations in the mountains, 10,000–14,000 feet elevation. Irregularly from the Alps of Europe, across Asia to

Alaska and south in the Rocky Mountains to northern New Mexico. June to August.

*Eritrichium* as here considered is a highly variable and widespread circumboreal species, with several varieties. In our flora only variety *elongatum* occurs and is limited to only the highest mountain peaks in northern New Mexico.

### 17. LAPPULA Gilib.

### Stickseed

Annual or biennial herbs; *stems* ascending or erect; *leaves* alternate, entire, narrow, firm, and veinless; *inflorescence* terminal, the flowers borne in a sympodial, branched cyme; *calyx* 5-parted, nearly to the base, accrescent; *pedicels* usually erect, short; *corolla* blue or white, rather inconspicuous, more or less funnelform, with conspicuous fornices; *stamens* included; variously inserted; *style* included; *nutlets* 4, ovoid to oblong, trigonous or flattened, with 1–3 rows of cylindrical, conical or flattened spines or glochidia on the sides, or on the cupulate border, attached to the elongate gynobase only part of their length.

A genus of about 10 species of wide distribution in the northern hemisphere (diminutive of the Latin lappa, a bur.)

#### Reference

Johnston, I. M. Studies in the Boraginaceae. A synopsis of the American native and immigrant borages of the subfamily Boraginoidae. Contr. Gray Herb. 70: 47–51. 1924.

1. Nutlets with 2 rows of slender marginal prickles that are not confluent at base; corolla about 3 mm broad .......... 1. *L. echinata*

— Nutlets with a single row of marginal prickles that are more or less confluent at the base; corolla 2 mm or less broad .......... 2. *L. redowskii*

1. **Lappula echinata** Gilib

*Myosotis lappula* L. Sp. Pl. 131. 1753. *Lappula myosotis* Moench. Meth. 417. 1794. *Echinospermum lappula* Lehm. Asperif. 121. 1818. *Lappula lappula* Karst. Deuts. Fl. 979. 1882. (*Europe*)

*Lappula echinata* Gilib. Fl. Lithu. 1: 25. 1781. (*Europe*)

*Echinospermum fremontii* Torr. Pacif. R. R. Reports 12: 46. 1860. *Lappula fremontii* E. L. Greene, Pittonia 4: 96. 1899. (*Fremont 844*, Pass Creek, near southern end of the Sierra Nevada)

*Stems* simple to freely branched, 1.5–8 dm tall, villous-hirsute; *leaves* linear to linear-lanceolate or lanceolate, acute or obtuse, narrowed to a sessile base, 2–5 cm long, 2–7 mm broad, hispidulous; *calyx* 2.5–3(4) mm long in fruit, the segments linear, appressed hispidulous; *pedicels* 1–3 mm long, erect; *corolla* bright blue, 2–4 mm broad; *nutlets* 3–4 mm long, sharply verrucose or muricate dorsally, with 2 marginal rows of long, slender bristles that are distinct to near the base, these sometimes irregularly distributed over the back.

Dry plains, hillsides, roadsides and waste places, also cultivated ground. Native to Eurasia, but widespread as a weed in northern United States and Canada. June to August.

*L. echinata* is rare in our flora, known only from Schultz Pass, Coconino County, Arizona (*Whiting 1173B*).

2. **Lappula redowskii** (Hornem.) E. L. Greene

*Myosotis redowskii* Hornem. Hort. Bot. Hafn. 1: 174. 1813. *Echinospermum redowskii* Lehm. Asperif. 127. 1818. (*Russia*)

*Echinospermum texanum* Scheele, Linnea 25: 260. 1852. *Lappula texana* Britt. Mem. Torrey Club. 5: 273. 1894. *L. redowskii* var. *texana* Brand, Pflanzenr. IV 252 (Heft. 97): 150. 1931. (*Roemer*, San Antonio, Texas) = var. *cupulata*

*Echinospermum redowskii* var. *occidentale* S. Wats. Bot. King Exp. 246. 1871. *Lappula redowskii* var. *occidentale* Rydb. Contr. U. S. Natl. Herb. 3: 170. 1895. *L. occidentalis* E. L. Greene, Pittonia 4: 97. 1899. *E. occidentale* K. Schum. Just. Bot. Jahresb. 27: 522. 1901. (S. *Watson 861*, from the Sierra's to the Wasatch) = var. *redowskii*

*Echinospermum redowskii* var. *cupulatum* A. Gray, Bot. Calif. 1: 530. 1876. *Lappula cupulata* Rydb. Bull. Torrey Club 28: 31. 1901. *Echinospermum cupulatum* K. Schum. Just. Bot. Jahresb. 29: 564. 1903. *L. redowskii* var. *cupulata* M. E. Jones, Bull. Univ. Mont. Biol. 15: 44. 1910. (S. *Watson 862*, Trinity Mountains, Nevada)

*Lappula desertorum* E. L. Greene, Pittonia 4: 95. 1899. *Echinospermum desertorum* K. Schum. Just. Bot. Jahresb. 27: 522. 1901. *L. redowskii* var. *desertorum* I. M. Johnst. Contr. Arnold Arb.r 3: 93. 1932. (*E. L. Greene*, near Holborn, Nevada, 16 July 1896)

*Lappula heterosperma* E. L. Greene, Pittonia 4: 94. 1899. *L. texana* var. *heterosperma* Nels. & Macbr. Bot. Gaz. 61: 41. 1916. (*Baker, Earle, & Tracy* 826, from near Mancos, in southwestern Colorado) = var. *cupulata*

*Lappula coronata* E. L. Greene, Pittonia 4: 94. 1899. *Echinospermum coronatum* K. Schum. Just. Bot. Jahresb. 27: 522. 1901. *L. texana* var. *coronata* Nels. & Macbr. Bot. Gaz. 61: 41. 1916. (*C. G. Pringle*, mesas near Tucson, Arizona, 18 April 1884) = var. *cupulata*

*L. leucotricha* Rydb. Bull. Torrey Club. 36: 676. 1909. (*Toumey*, near Tucson, Arizona, 20 April 1894)

*Stems* usually simple, or with several minor stems arising from the base of the major stem, or bushy branched from the base, 1–5 dm tall, cinereous hispid-villous; *leaves* narrowly oblanceolate to spathulate, the basal ones 1.5–5(8) cm long, 3–8 mm broad, rosettelike, the cauline leaves gradually reduced in size upward; *inflorescence* cymose, the individual racemes terminating the stems and branches; *bracts* conspicuous, subtending each flower; *calyx* in fruit 3–5 mm long, the segments linear or linear-lanceolate, strigose; *pedicels* erect or ascending 1–3 mm long; *corolla* blue or whitish, 1–2 mm broad; *nutlets* 2–3 mm long, muricate dorsally, with a single row of nearly distinct prickles, or sometimes with a greatly swollen cupulate border.

A weed in dry, usually disturbed areas along roadsides, abandoned fields and waste places. Eurasia and western North America. March to July.

*Lappula redowskii* is a widespread and variable species. Many names have been placed on the various forms that occur throughout the range of the species. The most distinct of these forms has been called *L. texana*, and, if it weren't for the many intermediate characteristics between it and the typical *L. redowskii*, it could easily be maintained as a distinct species. It is the many named and nameless forms that occur between these two extremes that have produced the abundant synonymy.

## 18. HACKELIA Opiz.

### Stickseed

Ascending or erect biennial or perennial herbs; *leaves* alternate, broad and veiny; *flowers* in naked or only basally bracteate scorpioid cymes paniculately disposed; *calyx* cut to the base into spreading ovate to oblong or lanceolate lobes; *pedicels* slender, recurving in fruit; *corolla* white or blue, with a short or elongated tube, and an evidently 5-lobed limb, the lobes rounded and connate less than one-third their length; *fornices* well developed; *stamens* included, affixed at middle of tube; *filaments* slender, short; *anthers* oblong to elliptic; *style* slender, scarcely if at all surpassing the nutlets; *stigma* capitate; *nutlets* 4, erect, ovate to lanceolate, attached ventrally to the pyramidal gynobase by a broad medial or submedial areola, the margin with subulate glochidiate prickles which are frequently confluent at the base, the back smooth or with glochidiate appendages.

A genus containing about 45 species, centering in western North America with outlying species in South America and Eurasia.

### References

Gentry, J. L. 1974. Studies in the genus *Hackelia* (Boraginaceae) in the western United States and Mexico. Southwestern Nat. 19:139–146.

Gentry, J. L. and R. L. Carr. 1976. A revision of the genus *Hackelia* (Boraginaceae). Mem. New York Bot. Gard. vol. 26, no. 1.

1. Corolla limb white to ochroleucous to greenish tinged .............................. 1. *H. ursina*

— Corolla limb blue or occasionally violet blue or pink .............................................. 2

2(1). Intramarginal prickles absent on all nutlets (or rarely present on *H. floribunda* and then only on less than half the nutlets) .............................................. 3

— Intermarginal prickles present on all nutlets .......................................... 4. *H. pinetorum*

3(2). Corolla limb inconspicuous, only 1.5–2.5 mm wide, calyx segments ca. 1 mm long .............................................................................................. 2. *H. besseyi*

— Corolla limb broader, mostly 4–8 mm wide; calyx segments mostly 1.5 mm long or more ........ 4

4(3). Cymes conspicuously bracteate throughout; cauline leaves long ciliate; stems generally stiffly hirsute ........ 3. *H. hirsuta*

— Cymes bracteate, if at all, only at the base; cauline leaves not long ciliate; stems with appressed hairs ........ 5

5(4). Fornices curved inward at the tips, about twice as long as broad; principal marginal prickles of all mature nutlets less than 2 mm long; inflorescence open and spreading, the branches few; plants slender ........ 4. *H. pinetorum*

— Fornices relatively straight, not curving inward at the tip, about as broad as long; principal marginal prickles more than 2 mm long; inflorescence mostly elongate and narrow ........ 5. *H. floribunda*

1. **Hackelia ursina** (Greene ex A. Gray) I. M. Johnston

*Echinospermum ursinum* Greene ex A. Gray, Proc. Amer. Acad. Arts 17: 224. 1882. *Lappula ursina* E. L. Greene, Pittonia 2: 182. 1891. *Hackelia ursina* I. M. Johnst. Contr. Gray Herb. 68: 46. 1923. (*E. L. Greene*, on gravel beds of Bear Canyon in the Bear Mountains, New Mexico, 4 October 1880)

*Lappula leucantha* E. L. Greene, Leafl. Bot. Observ. Crit. 1: 152. 1905. (*O. B. Metcalfe 1475*, Shady Canyon of Iron Creek, Black Range, Grant County, New Mexico, 11 October 1904) = var. *ursina*

*L. pustulata* Macbride, Contr. Gray. Herb. 48: 39. 1916. *Hackelia ursina* var. *pustulata* J. L. Gentry, Southwestern Naturalist 19(2):144. 1974. (*C. G. Pringle 563*, hills west of Chihuahua, Mexico, 23 October 1885)

*L. heliocarpa* Brand, Feddes Repert. Spec. Nov. Regni. Veg. 18: 310. 1922. *Hackelia heliocarpa* Brand, Pflanzenr. IV 252 (Heft. 97) 120. 1931. (*C. G. Pringle 2004*, Canyon below Cusihuiriachic, Chihuahua, Mexico, 21 September 1888) = var. *pustulata*

*Hackelia ursina* var. *diaboli* J. L. Gentry, Southwestern Naturalist 19(2):143. 1974. (*G. J. Harrison 1880*, Devil's Canyon, Pinal County, Arizona 16 May 1926) = var. *diaboli*

*Stems* erect, 1–several, sometimes branched near the base, 3–14 dm tall, hispid or hirsute with spreading bristles or often appressed strigose also, especially above; *leaves* at the base of plant oblanceolate, long petiolate, obtuse, 2.5–14 cm long, 5–15 mm broad, hispid-hirsute, pustulate, the cauline leaves gradually reduced above, oblanceolate to narrowly ovate, broader than the basal ones; *inflorescence* open and spreading; *bracts* evident throughout the cymes; *calyx* 1.5–3.5 mm long in fruit, the segments oblong to lanceolate, hispid; *pedicels* 1.5–10 mm long; *corolla* white or tinged with yellow, the tube 1.5–2.5 mm long, the limb 5–11 mm wide; *fornices* evident, papillate; *style* 0.8–1.8 mm long, longer than nutlet; *nutlets* 2–3 mm long, ovate to lanceolate, intermarginal prickles present or lacking, marginal prickles 7–11 on each side, slightly connate at the base or fused for half their length into a cupulate wing, dorsal surface muricate-hispidulous to nearly smooth.

Gravelly creek beds, rocky terraces, canyons, and talus slopes or moist areas, 3,500–8,500 feet elevation, mostly in the oak, juniper, or pinus communities. Southern Arizona, New Mexico, and northern Mexico. May to August.

Our plants of *H. ursina*, as here described, are the only white-flowered species and can be separated into three varieties by the following key:

1. Nutlets 2–2.5 mm long, with marginal prickles 1–2 mm long; flowering July and August; Pinal Mountains, Arizona, and western New Mexico to northern Mexico ........ 2

— Nutlets 2.5–3.5 mm long, with marginal prickles 2–3 mm long; flowering in May; rare in Devil's Canyon, Pinal County, Arizona ........ var. *diaboli* J. L. Gentry

2(1). Corolla limb 5–7.5 mm broad; pedicels rarely more than 2.5 mm at anthesis; southwestern New Mexico ........................................ var. *ursina*

— Corolla limb 7.5–10 mm broad; pedicels mostly more than 3 mm at anthesis; Pinal Mountains, Arizona, and northern Mexico ........................................ var. *pustulata* (Macbr.) J. L. Gentry

2. **Hackelia besseyi** (Rydb.) J. L. Gentry

*Lappula besseyi* Rydb. Bull. Torrey Club 31: 636. 1904. *H. leptophylla* var. *besseyi* Brand, Pflanzenr. IV 252 (Heft. 97): 127. 1931. *H. besseyi* Gentry, Southwestern Naturalist 19(2):139. 1974. (*C. E. Bessey*, mouth of Cheyenne Canyon, Colorado, 25 July 1895)

*L. grisea* Woot. & Standl. Contr. U. S. Natl. Herb. 16: 164. 1913. *H. grisea* I. M. Johnst. J. Arnold Arbor. 16: 194. 1935. (*E. O. Wooton*, James Canyon, Sacramento Mountains, New Mexico, 6 August 1905)

*Stems* erect, solitary, 3–11 dm tall, canescent with strigose or villous-hirsute hairs; *leaves* at base of plant oblanceolate, 2–9 cm long, (7)10–17 mm broad, obtuse, strigose to hirsute-hispid, pustulate, cauline leaves gradually reduced above 2–13 cm long, 5–10(12) mm broad; *inflorescence* open and spreading; *bracts* evident only near base of cyme; *calyx* 1–1.5 mm long in fruit, the segments lance-ovate; *pedicels* in fruit 3–5 mm long; *corolla* tube 0.8–0.9 mm long, limb 1.5–2.5 mm broad, blue; *fornices* evident, papillate; *style* shorter than nutlet; *nutlets* 2–2.5 mm long, ovate to ovate-lanceolate, intramarginal prickles lacking, marginal prickles 8–13 on each side, distinct or slightly connate, a long and short prickle alternating, dorsal surface muricate-hispidulous.

In the foothills, extending to moderate elevations in the mountains, 6,000–9,000 feet, in association with Pinyon-Juniper and Fir-Pine stands. El Paso County, Colorado, south through New Mexico to Trans-Pecos Texas. July to September.

The very small corollas, with ascending lobes, easily distinguish this plant from all other members of *Hackelia* in North America.

3. **Hackelia hirsuta** (Woot. & Standl.) I. M. Johnston

*Lappula hirsuta* Woot. & Standl. Contr. U. S. Natl. Herb. 16: 164. 1913. *H. hirsuta* I. M. Johnst. Contr. Gray Herb. 68: 46. 1923. (*G. Heller 3793*, 9 miles east of Santa Fe, New Mexico, 2 July 1897)

*Stems* 1 or few, often bluish tinged at the base, erect, or widely branched from the base and throughout, 1–8 dm tall, spreading hispid below, hirsute to strigose above; *leaves* at base of plant oblanceolate, acute, petiolate, withering early, 2–7 cm long, 5–10 mm broad, villous-strigose to hirsute, ciliate on the petioles, moderately pustulate, cauline leaves oblanceolate to linear-oblong, 3–10 cm long, 5–12 mm wide, ciliate; *inflorescence* open, widely spreading; *bracts* 3–10 mm long, evident throughout; *calyx* 2–3 mm long in fruit, the segments oblong to lanceolate; *pedicels* 5–10 mm long in fruit; *corolla* blue with a white eye, the tube 1.5–2 mm long, limb 4–8 mm broad; *fornices* evident, papillate; *style* 0.6–1.1 mm long, shorter than nutlet; *nutlets* 2.5–3.5 mm long, ovate-lanceolate, intramarginal prickles absent, marginal prickles 4–7 on each side, slightly connate or distinct at the base, dorsal surface muricate-hispidulous.

On dry, open hillsides or shale roadcuts, in oak canyons or coniferous forests, or rarely moist areas, 6,000–10,000 feet elevation. Endemic to north central New Mexico.

A striking and very distinct species due to the spreading branches and the conspicuously hirsute-hispid stems and leaves.

4. **Hackelia pinetorum** (Greene ex A. Gray) I. M. Johnston

*Echinospermum pinetorum* Greene ex A. Gray, Proc. Amer. Acad. Arts 17: 224. 1882. *Lappula pinetorum* I. M. Johnst. Contr. Gray Herb. 68: 45. 1923. *H. floribunda* var. *pinetorum* Brand, Pflanzenr. IV 252 (Heft. 97): 127. 1931. (*E. L. Greene*, Pinos Altos Mountains, New Mexico, July and September 1880) = var. *pinetorum*

*H. pinetorum* var. *jonesii* J. L. Gentry, Southwestern Naturalist 19(2):142. 1974 (*M. E. Jones*, Soldier Canyon, Sierra Madre, Chihuahua, Mexico, 16 September 1903) = var. *jonesii*

*Stems* 1 or few, erect, 3–8 dm tall, grayish hirsute below, becoming strigose above; *leaves* at base of plant withering early, elliptic to oblong or oblanceolate, obtuse, petiolate, 3–8.5 cm long, 10–20 mm broad, hirsute to hispidulous, cauline leaves reduced upward, 3–12 cm long, 8–25 mm broad; *inflorescence* open and spreading; *bracts* lacking or 1–2 at the base; *calyx* 1.5–2 mm long in fruit, the segments lanceolate to oblong; *pedicels* 2–5 mm long in fruit; *corolla* pale blue, tube 1.3–1.6 mm long, the limb 4–7 mm broad; *style* not exceeding nutlet; *nutlets* 2–3 mm long, lanceolate to lance-ovate, intramarginal prickles small, 1–3 or absent, marginal prickles 4–7 on each side, distinct or slightly connate at the base, less than 2 mm long, dorsal surface muricate hispidulous.

Moist, shaded places in Douglas-fir or oak woods or pine woodlands at elevations 6,000–9,000 feet. Coconino County, Arizona, south to southeastern Arizona to southern New Mexico and Trans-Pecos Texas, south into Chihuahua, Sierra Madre, Occidentale, Mexico. June to August.

The northern phase of *H. pinetorum* is the most common and is var. *pinetorum*. The southern element has been called var. *jonesii* and enters our flora only in the Organ Mountains of southern New Mexico. It is distinguished from the typical plant by the absence of intramarginal prickles; however, there is some introgression between the two varieties in the Organ Mountains.

5. **Hackelia floribunda** (Lehm.) I. M. Johnston

*Echinospermum floribundum* Lehm. Stirip. Pug. 2: 24. 1830. *E. deflexum* var. *floribundum* S. Wats. Bot. King Exp. 245. 1871. *Lappula floribunda* E. L. Greene, Pittonia 2: 182. 1891. *H. floribunda* I. M. Johnston. Contr. Gray Herb. 68: 46. 1923. (*Drummond*, Saskatchewan)

*Lappula leptophylla* Rydb. Mem. New York Bot. Gard. 1: 329. 1900. *H. leptophylla* I. M. Johnst. Contr. Gray Herb. 68: 46. 1923. (Several specimens cited from Montana and Wyoming)

*Stems* stout, erect, 5–12(14) dm tall, reflexed or spreading hirsute or strigose below; *leaves* at base of plant withering early, oblanceolate to elliptic-oblong, 4–20 cm long, 5–20(25) mm broad, petiolate, apex obtuse to acute, hirsutulous-appressed, cauline leaves sessile, gradually reduced upward; *inflorescence* elongate, rather narrow with strongly ascending, many-flowered branches; *bracts* lacking or 1–2 at base of cymes; *calyx* in fruit 2–3(3.5) mm long, the segments oblong to lance-oblong, hirsute; *pedicels* 1–3.5 mm long at anthesis, in fruit becoming 4–7(10) mm long; *corolla* blue or rarely whitish, the tube 1–2 mm long, the limb 4–7 mm broad; *fornices* small, obscurely papillate; *style* shorter than nutlets; *nutlets* 3–5 mm long, ovate or ovate-lanceolate, intramarginal prickles lacking or rarely present on a few of the nutlets of the inflorescence, marginal prickles 5–8 on each side, distinct or slightly connate, or sometimes fused for half their length, 1.5–3 mm long, dorsal surface with a faint median ridge, muriculate-hirsutulous.

Moist to moderately dry places in the mountains or foothills, or along stream banks, associated with oak, aspen, and evergreen forests 4,000–10,500 feet elevation. British Columbia, Alberta, and Saskatchewan, south to Nevada, Arizona, and New Mexico. Disjunct to Durango, Mexico, less often in Washington, Oregon, and California. July to August.

There is some variation within *H. floribunda*, such as the fusion of marginal prickles or not, and the presence or absence of intramarginal prickles. These phases in the past have been called *H. leptophylla*; however, they seem to be wholly arbitrary and not worthy of any taxonomic recognition.

# ANOMIOPSYLLINAE (SIPHONAPTERA: HYSTRICHOPSYLLIDAE), II. THE GENERA *CALLISTOPSYLLUS*, *CONORHINOPSYLLA*, *MEGARTHROGLOSSUS*, AND *STENISTOMERA*

Vernon J. Tipton[1], Harold E. Stark,[2], John A. Wildie[3]

Abstract.— The subfamily Anomiopsyllinae in North America consists of five genera: *Anomiopsyllus* Baker; *Callistopsyllus* Jordan and Rothschild; *Conorhinopsylla* Stewart; *Megarthroglossus* Jordan and Rothschild; and *Stenistomera* Rothschild. The revision of *Anomiopsyllus* was the subject of a previous paper, and the remaining four genera are treated herein. The North American genus *Jordanopsylla* Traub and Tipton and the Palearctic genus *Wagnerina* Ioff and Argyropulo had been included in the subfamily Anomiopsyllinae by Ioff and Argyropulo, but these two genera possess characters which are not consistent with the current definition of the subfamily. All species are considered to be "nest fleas," but modifications for a nest habitat are more pronounced in some species than others. Diagnoses, descriptions, and keys are given for genera and most species. In addition, illustrations, host records, and geographical distribution are given for each of the 21 species.

The family Hystrichopsyllidae Tiraboschi, 1904, consists of nine subfamilies. In four of the subfamilies (Acedestiinae, Ctenophthalminae, Dinopsyllinae, and Stenoponiinae) genal combs are present. In three additional subfamilies genal combs are present except in certain genera (Hystrichopsyllinae except *Atyphloceras*, Neopsyllinae except *Catallagia* and *Delotelis*, and Rhadinopsyllinae except *Wenzella* and *Trichopsylloides*). There is no genal comb in the subfamily Anomiopsyllinae, and it is vestigial or lacking in Listropsyllinae. In Anomiopsyllinae the eye is reduced, vestigial, or absent. The pleural arch is absent, the lateral metanotal area is reduced or absent, the upper anterior margin of the metepisternum is concave, and there is no striarium on abdominal segment II. There is marked reduction in chaetotaxy in *Anomiopsyllus*, not marked in *Stenistomera*, and intermediate in the other three genera of the subfamily.

Anomiopsyllinae in North America consists of five genera: *Anomiopsyllus* Baker; *Callistopsyllus* Jordan and Rothschild; *Conorhinopsylla* Stewart; *Megarthroglossus* Jordan and Rothschild; and *Stenistomera* Rothschild. The genus *Anomiopsyllus* was revised by Barnes, Tipton, and Wildie (1977) in the first of a series of papers on the family Hystrichopsyllidae. The remaining four North American genera are discussed in this paper.

When Traub and Tipton (1951) described the genus *Jordanopsylla*, they indicated that it differed from the other genera of Anomiopsyllinae as follows: "The metephimere is free; the pleural arch is present; the upper margin of the metepisternum is convex; and the internal marginal tubercle of the metepisternum is vestigial." Based on these differences they erected the tribe Jordanopsyllini. Ioff and Scalon (1954) recognized the morphological similarities between *Jordanopsylla* and *Wagnerina* Ioff and Argyropulo and placed the latter with *Jordanopsylla* in the tribe Jordanopsyllini. The characters given above provide ample reason to question inclusion of these two genera in the subfamily Anomiopsyllinae.

*Eopsylla* Argyropulo, like *Wagnerina*, is palearctic in distribution and so will not be considered here.

The five North American genera of Anomiopsyllinae exhibit ecological as well as morphological affinities. Their morphological similarities reflect their shared evolutionary history and habitat. They are considered "nest fleas," which means they are better adapted to conditions in the nest than on the

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host. Traub (1972) listed characters which appear to be common to nest fleas, and all five genera possess these characters in varying degrees. The genus *Anomiopsyllus* appears to have better adapted to the nest environment than other genera of the subfamily. The outstanding features of *Anomiopsyllus* anatomy that appear to be adaptive are "complete eyelessness, extreme reduction in number of setae and spines, extensive loss and fusion of structures in the metathorax, and loss of structures in both meso- and metacoxae." In contrast to the highly modified nature of the thorax, the abdominal segments are only moderately specialized, though marked by loss of some structures in the male genitalia" (Barnes et al. 1977). Other nest fleas share most of these morphological characters. If *Anomiopsyllus* represents the extreme in adaptation to nest conditions, *Stenistomera* may represent a more moderate adaptive position in that it has well-developed setation, including a comb on the mesotibia.

## DISCUSSION

Species density of fleas is much greater in the western half of the United States than in the eastern half. Hubbard (1947) indicated there were 33 genera and 56 species and subspecies of fleas known from east of the 100th meridian, and 67 genera and 230 species and subspecies were known from west of the 100th meridian. In the intervening years since 1947 several taxa have been described and thus these figures have been adjusted upward. For example, Benton (in press) lists 67 species and subspecies of fleas in the United States east of the Mississippi River. Of the 33 genera listed by Hubbard 19 genera occur only west of the 100th meridian. If the line which divides "east" and "west" is moved east 138 miles to the 98th meridian, then 27 genera are exclusively western. By way of comparison, there are two genera that occur only in the east. Dice (1943) emphasized the great diversity of habitats in the western United States in that he lists 15 biotic provinces west of the Mississippi River, but only four east of the Mississippi River. Jellison (1979) has pointed out that diversity of habitat is reflected in the large number of species of rabbits, squirrels, and other host animals in the west.

Simpson (1964) calls attention to a west-east species gradient for mammals and uses the term *front* to denote an abrupt decline in species density along a species density gradient. He also points out that mean annual precipitation and topographical relief are the two main factors that contribute to fronts. The 100th meridian corresponds roughly with the 20-inch isohyet, and the high relief topography of the west contrasts sharply with the low relief of the plains states and the relatively low relief of the eastern United States.

In Utah, a state of high relief, there are approximately 115 species and subspecies of fleas in an area of about 85,000 square miles. Hopla (1979) estimates there are 40 species and subspecies of fleas in Kansas, a state of low relief with an area of slightly more than 82,000 square miles.

Traub (1979) cautioned that "while mean annual precipitation and topographical relief are of course highly important factors, one must also consider the geologic history of the two areas and the origins and dispersals (history, biogeography, phylogeny and evolution) of the respective host and siphonapteran faunas."

The distributional pattern of ectoparasites may be influenced by their life-style. Insect parasites which are parasitic during all stages of their life history and are host specific tend to have distributional patterns similar to their hosts. On the other hand, insect parasites with at least one free-living stage and which are not host specific often have distributional patterns somewhat different from those of their hosts. Fleas in the subfamily Anomiopsyllinae are characterized as "nest fleas." There are 35 recognized species and subspecies in the five North American genera, of which four genera (33 species) occur west of the 98th meridian only and one genus (*Conorhinopsylla*, 2 species) occurs only east of the 100th meridian. They have been collected from the nests of *Neotoma* species and other nest-building rodents; although a few specimens have been collected from species of *Ochotona*, *Spilogale*, and other nonrodent hosts.

## Key to North American Genera of Anomiopsyllinae (Males)

1. Pronotal comb absent; chaetotaxy greatly reduced; eye absent; caudoventral margin of coxae II and III with acuminate spur .................................... *Anomiopsyllus*

— Pronotal comb present; chaetotaxy variable; eye vestigial or absent; caudoventral margin of coxae II and III without acuminate spur ............................... 2

2(1). Sternum VIII greatly modified, spiniforms on distal apex; clasper elongate (Figs. 18, 19, 22, 23) ............................................................................ *Conorhinopsylla*

— Sternum VIII not modified, without spiniforms on distal portion; clasper not elongate ............................................................................................................... 3

3(2). Eye vestigial; sternum VIII covers more than one-half of distal arm of sternum IX; apex of movable process of clasper on a level with or extends only slightly dorsad of immovable process of clasper ............................................ *Megarthroglossus*

— Eye absent; sternum VIII covers less than one-half of distal arm of sternum IX; apex of movable process of clasper extends well beyond apex (dorsad) of immovable process of clasper ........................................................................................ 4

4(3). Frons evenly convex; dorsal margin of aedeagal apodeme not extended into long coiled rod; preantennal area and abdominal sterna lacking enlarged bristles; mesotibia without dorsolateral comb ......................................... *Callistopsyllus*

— Frons subacuminate; dorsal margin of aedeagal apodeme extended into long coiled rod; preantennal area and abdominal sterna possessing slightly or greatly enlarged bristles, mesotibia with dorsalateral comb ..................... *Stenistomera*

### *Callistopsyllus* Jordan and Rothschild

*Callistopsyllus* Jordan and Rothschild 1915:46 (Type species *Callistopsyllus terinus* Rothschild 1905 as *Ceratophyllus*); Ewing 1929:162; Jellison and Good 1942:26; Ewing and Fox 1943:102,111; Hubbard 1947:274,281; Holland 1949b:55,96; Traub and Tipton 1951:267–268; Traub and Hoff 1951:1–23; Jellison, Locker, and Bacon 1953:17; Hopkins 1957:64–87; Parker and Howell 1959:597–604; Hopkins and Rothschild 1962:354; Jellison and Glesne 1967:28–29; Lewis 1974:147–167.

*Callistopsyllus* was described by Jordan and Rothschild in 1915 and *Ceratophyllus terinus* Rothschild, 1905, was designated as type species. Since the original description, three new species have been described: *C. deuterus* Jordan, *C. campestris* Holland, and *C. paraterinus* Wagner, but the latter was subsequently placed as a junior synonym of *terinus*. Our study has demonstrated that morphologic differences are slight and intergrade in several geographic localities. It is considered advisable to regard *Callistopsyllus* as monotypic, with *deuterus* and *campestris* as subspecies of *C. terinus*. *Callistopsyllus terinus* is distributed widely over most of western North America. In recent correspondence, Traub (1978) expressed doubt that a single species of a nest flea would have such broad distribution. However, morphological characters used to separate described species are within the range of variation found in one locality, especially in New Mexico. The original description of *C. deuterus* matches the majority of specimens collected in eastern California and western Nevada. Reliable separation is difficult. Even the validity of subspecies is doubted, because the slight differences are not consistently correlated with geographic distribution. However, subspecific status is maintained at this time to preserve currently recognized names and to facilitate study of morphological variation. Specimens from Alberta and Saskatchewan have been described as *C. campestris*. At localities in Montana, Wyoming, and North Dakota, specimens bearing a resemblance to *campestris* have been found with typical *terinus*.

DIAGNOSIS.— There are two rows of preantennal bristles in *Callistopsyllus* and four rows in *Stenistomera*. *Callistopsyllus* may be separated from *Megarthroglossus* and *Conorhinopsylla* by the absence of an eye and from *Anomiopsyllus* by the presence of a pronotal comb. One of the most distinguishing characteristics of *Callistopsyllus* males is the very prominent movable process which greatly exceeds the length of the fixed process and is very large in relation to the comparatively small body. The movable process has two spiniform bristles, similar to those of *Stenistomera* and some *Anomiopsyllus* but unlike *Conorhinopsylla* and *Megarthroglossus*, which lack spiniform bristles.

DESCRIPTION.— HEAD: Interantennal suture present. Frontal tubercle present. Frontal margin evenly rounded. Eye absent. Head bristles not spiniform as in some *Stenistomera*. Two rows of preantennal (or preoccular) bristles; anteriormost row usually posterior to cibarial pump. Antenna of male enlarged greatly over that of female. Pedicel of antenna of male extends over part of club. Trabecula centralis absent. Antennal fossae extend to beyond posterior border of head. Anteroventral angle (oral angle) of head with sharp, small labrum. Maxillary lobe as in *Megarthroglossus*. Labial palp with 4 segments which extend beyond foretrochanter; apex more or less symmetrical; other members of Anomiopsyllinae with shorter labial palpi except *Megarthroglossus* which has 5 segments extending well beyond trochanter, with asymmetrical distal segment. Apex of genal lobe acute.

THORAX: Pronotal comb with 15–18 (usually 17) teeth on both sides, each sex. Pleural arch absent. Metasternum and metepimeron fused with metepisternum. Metepisternum lacks bristles. Lateral metanotal area absent. Metepimeron with spherical spiracle. Prosternum not distinctive, without bristles, triangular portion with apex directed posteriorly as in *Anomiopsyllus*. Mesosternum and mesepimeron with one long bristle each. Metanotum with about 11 large bristles on each side, about 4 tiny bristles between these. Mesonotum with one row of about 4 bristles on each side plus 3 pseudosetae.

LEGS: Coxae lack spurs as in *Anomiopsyllus*; coxa I with one long apical bristle; mesocoxa with partial longitudinal break; each femur with heavy, long, curved bristles at apex; none elsewhere on lateral surface; with small bristles along dorsal margin; mesotibia lacking comblike arrangement of setae as in *Stenistomera*. Metatarsus with 4 lateral, curved setae plus medially displaced proximal pair.

ABDOMEN: Segment II with spherical spiracle. Each abdominal segment with single row of bristles; tergum I with 3–4, terga II–IV with 5, and terga V–VI with 4 long bristles; abdominal tergum VII with 2–3 shorter bristles; 3 antepygidial bristles in both sexes, middle bristle longest, upper bristle shortest. Ventral sternum II with no bristles, sterna III–VII with 2–5 long bristles (2 in male). Abdominal tergum I with 3–5 (usually 4) apical spinelets on each side; abdominal tergum II with 1–4, III with 1–3 (usually 1), IV with 0–1 (usually 0) apical spinelets on each side.

*Modified Segments—Male*: Movable process extends dorsad beyond fixed process of clasper; with two blunt spiniform bristles. Caudal margin of sternum VIII rounded, not distinctively shaped; does not ensheathe sternum IX. Sternum IX shaped like neck and head of goose, beak pointed dorsad, with 10–12 short, thick setae directed caudad. Aedeagal apodeme extends as far cephalad as apex of manubrium or beyond; blade shaped, anterior and posterior ends curved slightly dorsad; neck constricted; dorsal margin with groove which receives ventral margin of manubrium. Median dorsal lobe small, distinct, as is crochet and apex of sclerotized inner tube. Penis rods long, coiled almost one full turn.

*Modified Segments—Female*: Caudal margin of sternum VII curved as in smooth arc, lacking lobes and sinuses. Anal stylet slender, almost 4 times as long as broad; apical seta long, with 2 tiny setae near apex; 1 dorsal, 1 ventral. Spermatheca with oval bulga; no collar. Length of hilla and bulga approximately equal.

### *Callistopsyllus terinus* (Fox)

*Ceratophyllus terinus* Rothschild 1905:158.

DIAGNOSIS.— Variations of taxonomic value are found only in male genitalia, primarily the movable process of the clasper. Remaining characters (of head, mouth parts, antennae, pronotum, legs, etc.) are as given in the preceding description and are found in specimens throughout the range of *C. terinus* ssp. The following discussion applies to variations or consistent characters of the three recognized subspecies of *C. terinus*. The purpose of the abbreviated form is to shorten the diagnosis given under each subspecies.

MALE: Fixed process of clasper low, convex, evenly rounded with single large bristle. Finger somewhat triangular, variable according to distribution and subspecies. Placement of two spiniforms varies, closely together in some specimens but more widely separated in others. No measurements were necessary since no pattern of placement is associated with recognized subspecies or with distribution. Distal arm of sternum IX paired, somewhat triangular. Caudal margin evenly convex except some specimens with slight notch, small thick bristle, other specimens (some *campestris* and some northern *terinus* in Idaho) with pronounced angle about midway. About 15 to 21 variously sized bristles along caudal margin and around apex. Some specimens (sometimes from single collections site) have unusually heavy bristles along caudal margins. The anterior portion is membranous. The proportions of the membranous anterior portions match the more sclerotized caudal portions; for example, the apices of most *deuterus* are more slender than either *terinus* or *campestris* with regard both to the membranous apex and the sclerotized caudal margins and structures between. The basal portion has distinctive sclerites. While their shape is complex, differences among the three subspecies are inconsistent and unreliable for subspecies discrimination. Sclerites of the aedeagus have little or no variation among specimens examined.

FEMALE: Variations are slight. Caudal margin of sternum XII smoothly curved, with no lobes, sinuses, or angles; sometimes fairly concave. Hilla is longer than, shorter than, or equals bulga. Duct of spermatheca sclerotized for almost entire distance between spermatheca and bursa copulatrix. Length of sclerotized portion varies among specimens and variations in length are of no diagnostic value.

The differences between subspecies of *terinus*, the only valid species of *Callistopsyllus*, are minor. However, they are sufficiently distinctive to allow construction of a key for males.

TABLE 1. Distribution of subspecies of *Callistopsyllus terinus*.

| AREA | *C. t. campestris* | *C. t. deuterus* | *C. t. terinus* |
|---|---|---|---|
| Arizona | | X | X |
| California | | X | X |
| Colorado | | X | X |
| Idaho | | | X |
| Montana | X | | X |
| Nevada | | X | X |
| New Mexico | | | X |
| Oregon | | X | X |
| South Dakota | | | X |
| Utah | | | X |
| Wyoming | X | | X |
| Baja California | | X | |
| Alberta | X | | |
| British Columbia | | | X |
| Saskatchewan | X | | |

### Key to subspecies of *Callistopsyllus terinus*

1. Males .......... 2

— Females .......... indistinguishable

2(1). Apex of movable process bluntly rounded, slightly tapered from base to apex; distributed from northern Great Plains to New Mexico .......... *campestris*

— Apex of movable process acutely rounded, markedly tapered from base to apex; distribution general .......... 3

3(2). Anterior border of movable process convex with widest portion just above base; distribution—Baja California, California, western Nevada .......... *deuterus*

— Movable process triangular, anterior margin with widest portion next to base; distribution—Sierra Nevada and east to central North America, Mexico north to northern Great Plains .......... terinus

### *Callistopsyllus terinus terinus* Rothschild
Figs. 4, 7, 10, 13, 14, 99

*Ceratophyllus terinus* Rothschild 1903:158; Baker 1905:134,151.

*Callistopsyllus paraterinus* Wagner 1940:465.

*Callistopsyllus terinus* Jordan and Rothschild 1915:46; Jellison and Good 1943:26; Ewing and Fox 1943:111; Hubbard 1947:281; Holland 1949b:96; Tipton and Allred 1951:105–114; Ecke and Johnson 1952:36; Jellison, Locker, and Bacon 1953:17; Morlan 1955: 93–125; Stark 1959:97; Hopkins and Rothschild 162:355; Glesne 1967:28; Allred 1968:75; Tipton and Saunders 1971:18; Jellison and Senger 1973:19; Lewis 1974:147–167; Egoscue 1976:476

TYPE HOST.— *Citellus columbianus*

TYPE LOCALITY.— Mable Lake, British Columbia, Canada.

TYPE SPECIMEN.— British Museum (Natural History), London, England.

DIAGNOSIS.— MALE: Finger triangular; broad toward base with narrow, rounded apex, anterior and caudal margins nearly always straight (Fig. 4). Caudal border of distal arm of sternum IX evenly rounded apex narrow. (Fig. 7).

TABLE 2. Host associations of *Callistopsyllus terinus* subspecies.

| HOST SPECIES | *C. t. campestris* | *C. t. deuterus* | *C. t. terinus* |
|---|---|---|---|
| *Dipodomys ordii* | X | | X |
| *Eutamias speciosus* | | X | |
| *Eutamias quadrivittatus inyoensis* | | X | |
| *Microtus montanus dutcheri* | | X | |
| *Microtus mordax sierrae* | | X | |
| *Neotoma* nest | | | X |
| *Perognathus* sp. | X | | |
| *Peromyscus* sp. | X | X | X |
| *Peromyscus boylii* | | | X |
| *Peromyscus crinitus* | | X | X |
| *Peromyscus eremicus* | | | X |
| *Peromyscus maniculatus* | X | X | X |
| *Peromyscus m. artemisiae* | | | X |
| *Peromyscus m. gambeli* | | | X |
| *Peromyscus m. osgoodi* | X | | X |
| *Peromyscus m. sonoriensis* | | X | X |
| *Peromyscus truei* | | X | X |
| *Spermophilus columbianus* | | | X |
| *Tamiasciurus hudsonicus albolimbatus* | | | X |

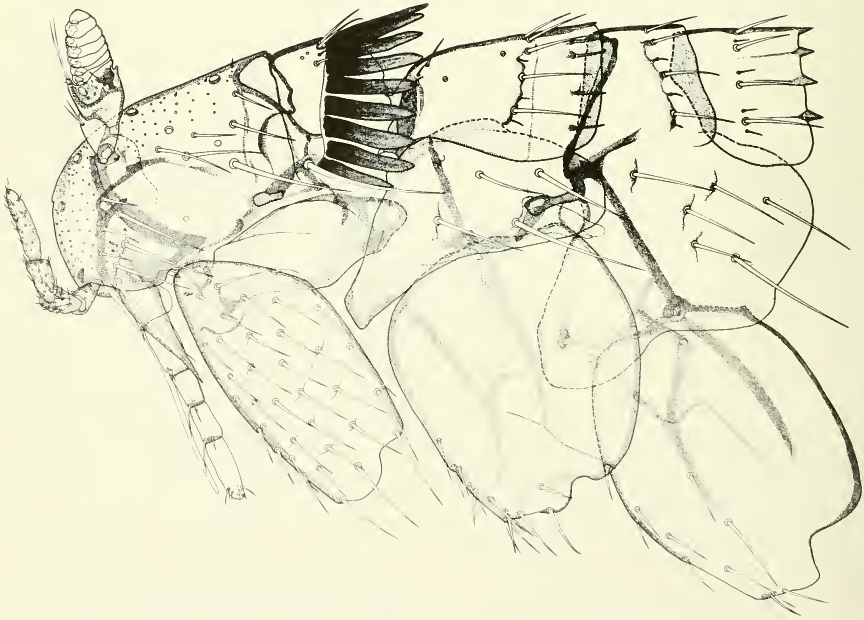
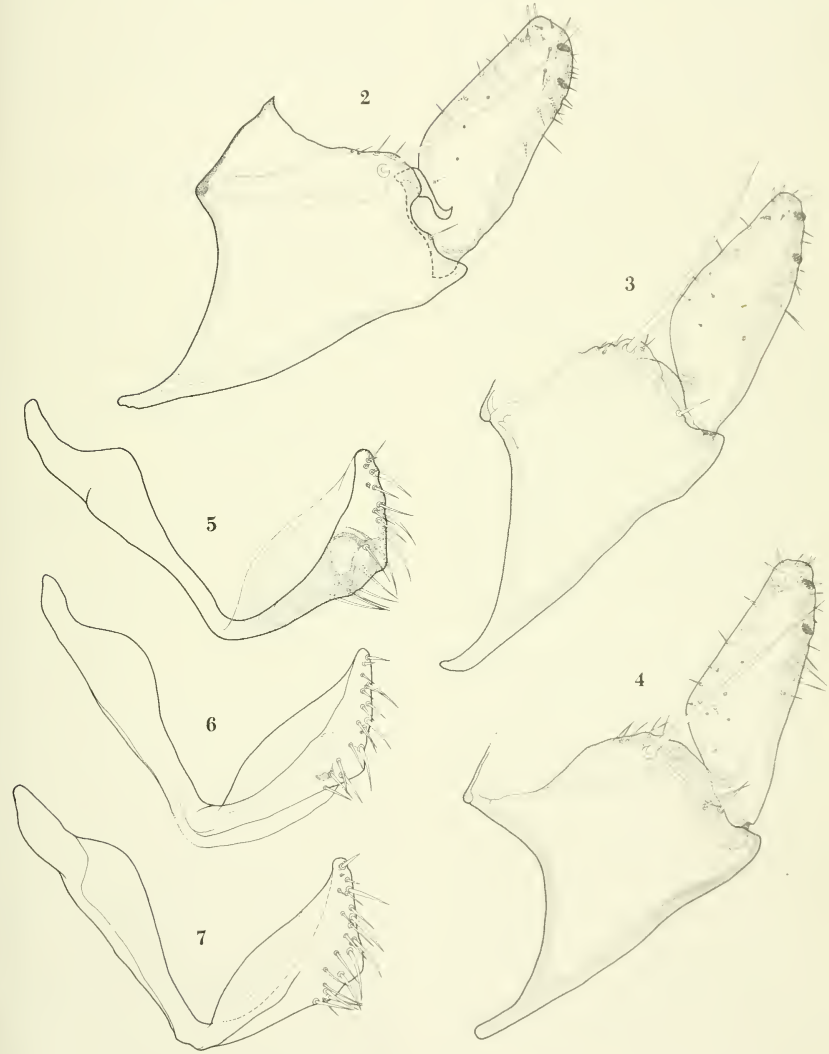


Fig. 1. *Callistopsyllus terinus deuterus*: Male, head and thorax including coxae.

FEMALE: Caudal margin of sternum VII faintly concave. Bulga of spermatheca about 1½ times as long as wide, shorter than hilla.

DISTRIBUTION.— ARIZONA: Coconino and Navajo Counties. BRITISH COLUMBIA: Eagle Pass, Dawson Falls, Marble Lake. CALIFORNIA: Nevada and Siskiyou counties. COLORADO: Larimer and Montezuma counties. IDAHO: Bingham, Butte, and Jefferson counties. MONTANA: Beaverhead, Park, and



Figs. 2–7. Males, claspers; 2, *Callistopsyllus terinus campestris*; 3, *C. t. deuterus*; 4, *C. t. terinus* Sternum IX; 5, *C. t. campestris*; 6, *C. t. deuterus*; 7, *C. t. terinus*.

Petroleum counties. Nevada: Douglas, Nye, and Washoe counties. New Mexico: Lincoln, Otero, Sandoval, San Juan, Santa Fe, and Taos counties. Oregon: Deschutes, Harney, and Jefferson counties. South Dakota: Custer County. Utah: Beaver, Box Elder, Daggett, Iron, Juab, Kane, Millard, Piute, Rich, San Juan, Tooele, Utah, Uintah, Wasatch, and Washington counties. Wyoming: Big Horn, Green River, Lincoln, Park, Sweetwater, and Weston counties.

Material Examined.— Arizona: (Coconino County) 3 ♂, 3 ♀, ex *Peromyscus truei* (TC-267), Tuba City, 23-I-1969; (Navajo County) 2 ♂, ex *Peromyscus truei* (B778), 31 km SW Holbrook, 26-IV-1949. Colorado: (Larimer Co.) 1 ♂, ex *Peromyscus maniculatus*, Rocky Mountain National Park, 7-VII-78; (Montezuma Co.) 2 ♂, ex *Peromyscus maniculatus*, Mesa Verde National Park, 26-V-1962; (Park Co.) 1 ♂, ex *Peromyscus maniculatus*, 3.2 km S Fairplay, 11-VIII-1949. Idaho: (Bingham Co.) 1 ♀, ex *Peromyscus maniculatus* (19Y) National Reactor Test Site (AEC-NRTS), 12-VIII-1966 (BYU); 1 ♀, same host, same location, 23-IX-1966 (BYU); 1 ♂, 1 ♀, ex rodent nest, AEC-NRTS (TRA), 11-X-1966 (BYU); 2 ♂, 3 ♀, ex *Peromyscus maniculatus*, AEC-NTRS (33y), 19-II-1967 (BYU); 1 ♀, ex *Neotoma* nest, AEC-NRTS (33Y), 10-III-1967; 1 ♂, 1 ♀, ex *Peromyscus maniculatus*, AEC-NRTS (19H), 3-VII-1967 (BYU); 1 ♂, 2 ♀, same host, AEC-NRTS (33Y), 20-VIII-1967 (BYU); (Butte Co.) 1 ♀, same host, AEC-NRTS (38Y), 19-II-1967 (BYU); 2 ♂, 1 ♀, same host, AEC-NRTS (36HF), 22-III-1967 (BYU). Nevada: (Nye Co.) 6 ♂, 7 ♀, ex *Peromyscus maniculatus* (334), 28 km NE Pahrump (Timber, Rocky Mt.) 19-XII-1949; (Washoe Co.) 1 ♀, ex *Peromyscus maniculatus* (44-E-16), 19-IV-1944. Oregon: (Jefferson Co.) 2 ♂, ex *Peromyscus* sp., Ames Ranch, Madras, 20-V-1958. New Mexico: (Lincoln Co.) 1 ♂, 3 ♀, ex *Peromyscus truei*, 3-IV-1948; (Otero Co.) 3 ♂, 1 ♀, ex *Peromyscus truei* (D443) 10 km E La Luz, Lincoln National Forest, 1300 m, 22-III-1949; 3 ♂, 1 ♀, 11 km NE La Luz, 1500 m, 24-III-1949; (San Juan Co.) 2 ♂, 1 ♀, ex *Peromyscus maniculatus* (B778), 73 km E Bloomfield, 1900 m, 18-V-1949; (Santa Fe Co.) 2 ♂, ex *Peromyscus maniculatus*, (4697) (697) Santa Fe, 2150 m, 2-IV-1953; (Taos Co.) 3 ♂, 1 ♀, ex *Peromyscus* sp., Pecos, 22-II-1941, McMurry (Jellison). (Some male specimens from New Mexico and the male from South Dakota are *terinus* near *campestris*.) South Dakota: (Custer Co.) 1 ♂, ex *Peromyscus maniculatus* (B1511), 45 km W Custer (1660 m, rock ledges, pine, juniper) 6-VI-1950. Utah: (Beaver Co.) 1 ♂, ex *Peromyscus maniculatus*, Puffer Lake, 25-VI-1957, D. M. Allred (BYU); (Box Elder Co.) 1 ♀, same host, Yost, George Creek, 9-VII-1957, D. M. Allred (BYU); (Daggett Co.) 2 ♂, 1 ♀, same host, Linwood, 15-VII-1954, C. L. Hayward (BYU); 1 ♀, ex *Dipodomys ordii*, Bridgeport, 1-VII-1954, C. L. Hayward (BYU); (Iron Co.) 1 ♂, ex *Peromyscus maniculatus*, Cedar Break National Monument, 21-VII-1953, D. E. Beck (BYU); (Juab Co.) 1 ♂, same host, Callao, 12-VIII-1953, Beck, Coffey, Killpack (BYU); (Kane Co.) 5 ♂, 5 ♀, ex *Peromyscus truei* (182), NAV-KAI, 2-XII-1971 (BYU); 2 ♀, ex *Peromyscus crinitus* (228), same location, 11-XII-1971 (BYU); (Millard Co.) 2 ♂, 1 ♀, ex *Peromyscus maniculatus*, Fillmore, 11-VII-1952, Killpack and Coffey (BYU); (Piute Co.) 1 ♀, same host, Marysvale, 27-VI-1952, Killpack and Beck (BYU); (Rich Co.) 1 ♀, same host, Monte Cristo R.S., 24-VI-1953, D. E. Beck; (San Juan Co.) 1 ♂, ex *Peromyscus* sp., VII-1946; (Tooele Co.) 1 ♂, ex *Peromyscus maniculatus*, Dugway Proving Ground (39), 2-VIII-1951; (Utah Co.) 1 ♂, same host, Goshen Springs, 10-IX-1965, W. J. Despain (BYU); (Uintah Co.) 1 ♂, 1 ♀, same host, Jensen, 9-VI-1953, D. E. Beck (BYU); (Wasatch Co.) 2 ♀, same host, Soapstone R.S., 31-VII-1948, Mulaik (BYU); 1 ♀, same host, Wallsburg, 2-VII-1953, D. E. Beck (BYU) ex *Peromyscus maniculatus osgoodi*, 1 ♂, 2 ♀, Strawberry Valley, 11-VI-64, K. B. Cox (BYU); (Washington Co.) 2 ♀, ex *Peromyscus eremicus*, Grafton, 17-XII-1950. Wyoming: (Big Horn Co.) 1 ♀, ex *Peromyscus maniculatus* (B-2762), 13 km NW Greybull, 7-VI-1940; (Green River Co.) 1 ♂, 1 ♀, ex *Peromyscus maniculatus* (G-862), 31.6 km NW Green River, 1908 m, 28-VI-1949; (Lincoln Co.) 1 ♀, ex *Peromyscus maniculatus*, Cumberland, 23-VII-1955; (Park Co.) 1 ♂, 1 ♀, ex *Peromyscus maniculatus* (C-2846-5), Yellowstone National Park, Old Faithful Lodge, 22-V-1940; 1 ♂ (Finger resembles both *terinus* and *campestris*.), ex

*Peromyscus maniculatus* (G-998), 41.7 km NW Cody, Shoshone National Forest, 2431 m (pine, cedar), 11-VIII-1949; (Sweetwater Co.) 1 ♀, ex *Peromyscus boylii* (B-1642), 17-VIII-1938; (Weston Co.) 1 ♂ (Finger resembles both *terinus* and *campestris*.), ex *Peromyscus maniculatus* (F-848), 10 km N Newcastle, 1385 m (pine bluffs), 26-V-1949.

HOST SYNONYMY.— *Tamiasciurus douglasi albolimbatus* = *Tamiasciurus hudsonicus albolimbatus.*

### *Callistopsyllus terinus deuterus* Jordan, new combination

Figs. 1, 3, 6, 8, 11, 14, 36, 97

*Callistopsyllus deuterus* Jordan 1937:266; Hubbard 1940:37(4); Auguston 1942a:140; Auguston, 1942b:150; Jellison and Good, 1942:26; Ewing and Fox, 1943:111; Hubbard 1943:1–12; Hubbard 1947:283; Hubbard 1949:126; Jellison, Locker, and Bacon 1953:17; Hopkins and Rothschild 1962:358; Beck 1966:76; Beck and Allred 1966:13; Stark and Kinney 1969:287–294; Lewis 1974: 147–167; Nelson and Smith 1976:51–61.

TYPE HOST.— *Peromyscus* sp.

TYPE LOCALITY.— Big Bear Lake, California.

TYPE SPECIMENS.— United States National Museum, Washington, D.C.

DIAGNOSIS.— MALE: Finger triangular; broad toward base with a narrow, round apex. Anterior margin convex with a rounded angle just above base. In *terinus* and *campestris* this angle is at base and is sharper. Caudal margin of finger of *deuterus* sometimes convex in apical half. Caudal margin of distal arm of sternum IX with rounded angle about midway, making apex appear narrower than in *terinus* or *campestris*. Small notches, thick bristles, and sharper angles found midway along the caudal border of distal arm of sternum IX of few specimens of *terinus* are not present in *deuterus* specimens available for examination. Apex of distal arm narrower and longer than either *terinus* or *campestris*, especially *campestris*.

FEMALE: Characters are not sufficiently distinctive to separate *deuterus* from *campestris* or *terinus*.

DISTRIBUTION.— ARIZONA: Yavapai County. CALIFORNIA: Fresno, Mariposa, Mono, Siskiyou, and Tuolumne counties. COLORADO: Montezuma County. MEXICO: Baja California. NEVADA: Nye County. OREGON: Jefferson County.

MATERIAL EXAMINED.— ARIZONA: (Yavapai Co.) 1 ♂, ex *Peromyscus truei* (B-708), 16.7 km N Prescott, 5-IV-1949 (The male is definitely *deuterus*, but other Arizona males are *terinus* (q.v.). The females from Yavapai Co. may be either *terinus* or *deuterus*.); 1 ♀, ex *Peromyscus truei* (B-717), 8.3 km N Prescott, 1662 m, 7-IV-1949; 1 ♀, ex *Peromyscus* sp. (A-301), 22-IV-1938. BAJA CALIFORNIA: 1 ♂, 1 ♀, ex *Peromyscus truei*, 1.6 km S. El Condor Hwy #2, 31-XII-1962, W. J. Wrenn (Traub Collection). CALIFORNIA: (Fresno Co.) 1 ♀, ex *Eutamias speciosus* (16097), Huntington Lake, 9-VI-1979; 1 ♀, ex *Peromyscus maniculatus* (16099), Huntington Lake (Bureau Vector Control, CA); (Mariposa Co.) 1 ♂, ex *Peromyscus* sp., Jct. Yosemite Creek Trail & Tioga Rd., Yosemite National Park, 2215 m, 2-VI-1959; (Mono Co.) 1 ♂, ex *Peromyscus maniculatus*, Tioga Pass Resort, Jct. Tioga Rd. & Saddle Bag Lake Rd., Inyo National Forest, 3077 m, 8-IX-1961; (Tuolumne Co.) 1 ♂, ex *Peromyscus maniculatus*, Tuolumne Meadows, Yosemite National Park, 2615 m, (Plague Lab); County not given: 1 ♂ (16478), locality not given (Bureau Vector Control, CA). NEVADA: (Nye Co.) 1 ♀, ex *Peromyscus crinitus*, Mercury (AEC-NRTS), 9-XII-1961 (BYU). OREGON: (Jefferson Co.) (See *C. t.* material examined).

### *Callistopsyllus terinus campestris* Holland, new combination

Figs. 2, 5, 9, 12, 14, 98

*Callistopsyllus campestris* Holland, 1949b:98; Hopkins and Rothschild, 1962:358; Senger, 1966:106; Jellison and Senger, 1973:19; Lewis, 1974:147–167.

TYPE HOST.— *Peromyscus maniculatus osgoodi.*

TYPE LOCALITY.— Medicine Hat, Alberta, Canada.

TYPE SPECIMENS.— Canadian National Collection, Ottawa, Canada.

DIAGNOSIS.— MALE: Finger somewhat rectangular or oval, depending upon specimen. Narrower basally and broader distally than in either *terinus* or *deuterus*; sides subparallel. Angle of anterior border at base variable; its outline is between that of *terinus*, which is acute and at the base, and *deuterus*, which is rounded and above the base. Distal arm of sternum IX gradually curved along curved margin; apex broadly rounded—more so than in *terinus* or *deuterus*. Bristles along caudal border of distal arm of sternum IX about as numerous (13–14) as *terinus*.

Female: Characters are not sufficiently distinctive to separate *terinus* from *deuterus* or *campestris*.

Distribution.—Alberta, Saskatchewan. Montana: Big Horn, Custer, and Park counties. Wyoming: Teton County.

Material examined.— Alberta: 1 ♂, 1 ♀, ex *Peromyscus maniculatus osgoodi*, Medicine Hat, 6-VI-40 (Holland). Saskatchewan: 1 ♂ ex *P. m. osgoodi*, Estevan, 28-VI-42 (Holland). Montana: (Custer Co.), 1 ♀, ex *Dipodomys ordii* (C-2574), 45 km S of Miles City, 22-III-1940; 1 ♂, ex *Peromyscus maniculatus* (C-2581-5), 28-III-1940; 1 ♀, ex *Peromyscus maniculatus* (C-2589-S), 29-III-1940; 2 ♂, ex *Peromyscus maniculatus* (C-2599), 42 km SW of Miles City, 30-III-1940; (Park City) 2 ♂, 1 ♀, ex *Peromyscus* sp., (D-667), 29-VI-1938; (Prairie Co.) 1 ♂, 1 ♀, ex *Peromyscus maniculatus* (E-760), 8 km E Terry (sage 677 m) 26-V-1949.

### *Conorhinopsylla* Stewart

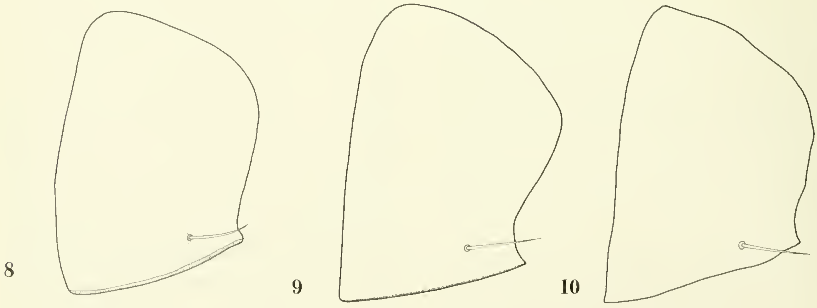
*Conorhinopsylla* Stewart 1930:178; Fox 1940:29, 41; Jellison and Good 1942:42; Ewing and Fox 1943:73; Jellison 1945:109–111; Hubbard 1947:274,293; Holland 1949b:55, 101; Traub and Tipton 1951:267–268; Jellison, Locker, and Bacon 1953:37; Hopkins 1957:64–87; Stark 1959:97; Hopkins and Rothschild 1962:359; Jellison and Glesne 1967:67; Lewis 1974:147–167.

Diagnosis.— *Conorhinopsylla* is the only genus in the subfamily in which the anteroventral angle of the head is acuminate, there is no clypeal tubercle, there are two rows of bristles on the terga, and the pleural arch is vestigial. The eye is vestigial as in *Megarthroglossus*, but in the latter genus there are no spiniform bristles on the genitalia. Male sternum VIII is greatly modified and bears spiniform bristles on the distal portion.

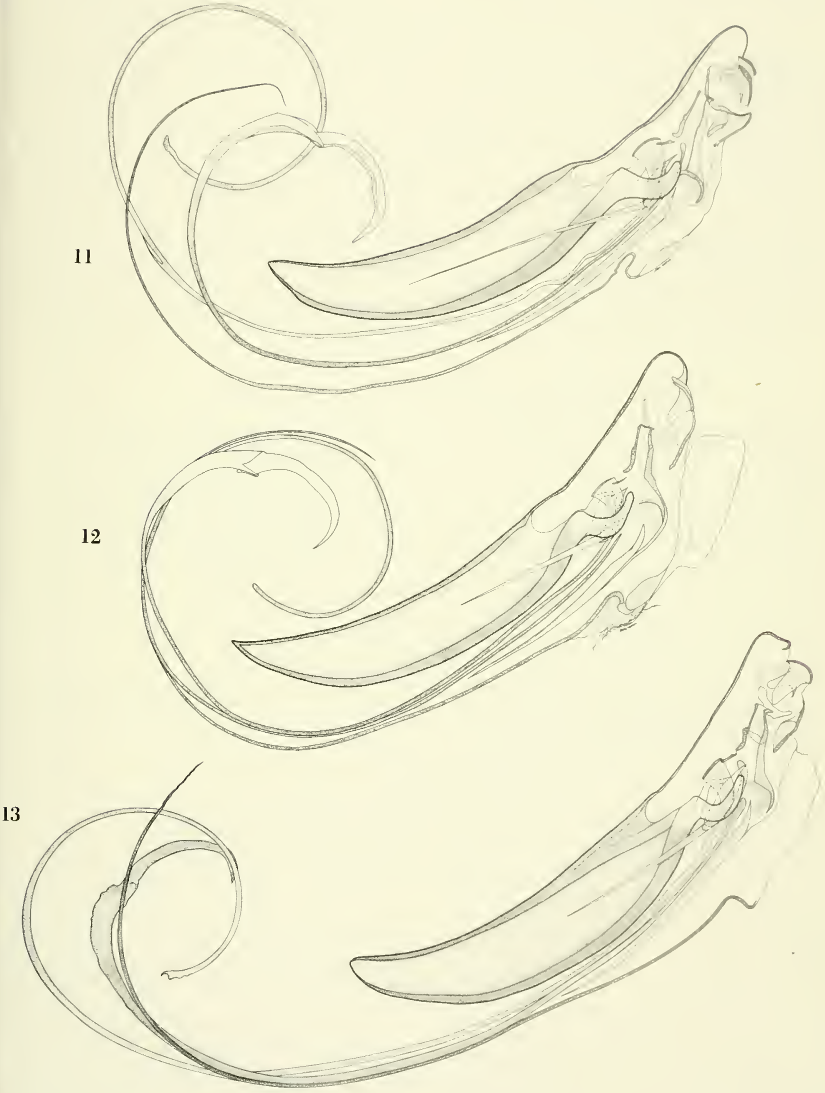
Description.— Head: Anterior margin of head slightly convex, frontal tubercle absent, oral angle a nipplelike protuberance. Genal process with undulating anterior margin, apex subtruncate to truncate. Two prominent ocular bristles near anterior margin of genal process. Irregular row of 5 preoccular bristles. Eye vestigial, triangular, lightly pigmented. Trabeculum centralis (area communis) absent. Antennal fossae do not extend to vertex to form interantennal suture; anterior margin with 3–4 small bristles; posterior margin with 4–5 small submarginal bristles. First and second antennal segments with several small bristles plus 5–6 small bristles. Occipital area with two large bristles; placoids on both frontal and occipital areas. Maxillary palp 4-segmented. Labial palp 5–8 segmented, extends beyond foretrochanter, apex asymmetrical. Genal comb absent.

Thorax: Pronotal comb with 12 very broad teeth. Pleural arch absent. Pleural rod very thin and elongate.

Legs: Sexual dimorphism in chaetotaxy of hind legs pronounced in *S. stanfordi*, less so



Figs. 8–10. Males, sternum VIII; 8, *Callistopsyllus terinus deuterus*; 9, *C. t. campestris*; 10, *C. t. terinus*.



Figs. 11–13. Males, aedeagus; 11, *Callistopsyllus terinus deuterus*; 12, *C. t. campestris*; 13, *C. t. terinus*.

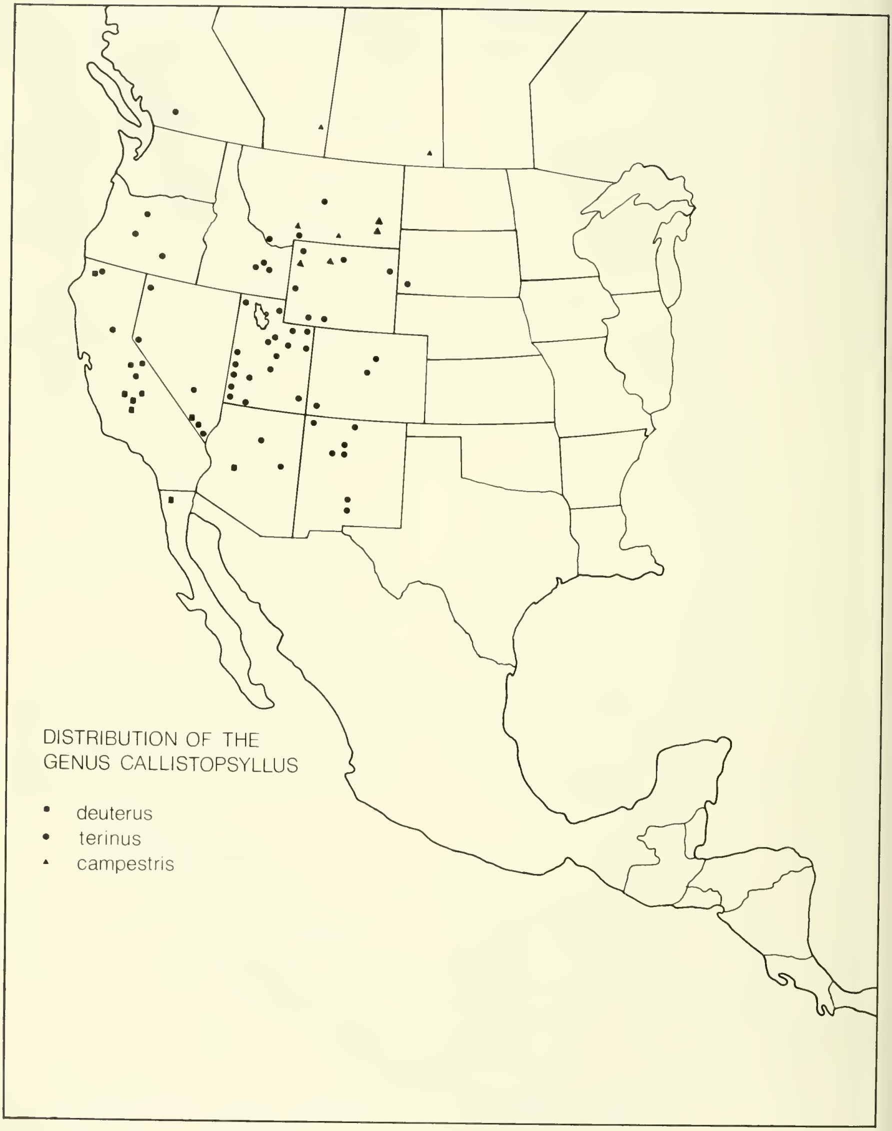

DISTRIBUTION OF THE
GENUS CALLISTOPSYLLUS
● deuterus
● terinus
▲ campestris

Fig. 14. Distribution of *Callistopsyllus terinus* ssp.

in *S. nidicola*. Four pairs of lateral plantar bristles and proximal median pair of bristles on fifth tarsal segments of all legs.

ABDOMEN: Abdominal tergal spinelets variable, generally terga I–III with 2 spinelets per side, tergum IV with one per side, terga V–VII without spinelets; each tergum with 1 row of bristles usually consisting of 5 to 7 long bristles intermixed with several minute bristles, ventrad most long bristle shifted anterad on main row of bristles. Lateral bristles on abdominal sterna variable, usually in row of 2–4 per side. Number of antepygidial bristles 2 or 3 depending on species: with 3, centermost longest, remaining 2 vary from minute to small in males or from two-thirds to three-fourths length of middle bristle in females; with 2, dorsal bristle longest, ventral bristle varies from minute to medium in males, from three-fourths to subequal in length to dorsal bristle in females.

*Modified segments—Male*: Fixed process of clasper greatly enlarged, modified in *C. stanfordi*, less so in *C. nidicola*. Sternum VIII reduced, with apical or subapical spiniform bristles. Sternum IX reduced, with apical and subapical bristles. Details of aedeagal morphology vary according to species.

*Modified segments—Female*: Caudal margin of sternum VII convex. Bulga of spermatheca somewhat beanlike, hilla lacking striations, otherwise lacking sharp line of demarcation between bulga and hilla.

## Key to The Species of *Conorhinopsylla* Males

| | | |
|---|---|---|
| 1. | Apical portion of distal arm of sternum VIII with 8 or more spiniform bristles (Fig. 19); movable process of clasper extends far beyond apex of immovable process of clasper (Fig. 23) ........................ | *nidicola* |
| — | Apical portion of distal arm of sternum VIII with 5 or fewer spiniform bristles (Fig. 18); movable process of clasper does not extend far beyond immovable process of clasper (Fig. 22) ........................ | *stanfordi* |

TABLE 3. Distribution of species of *Conorhinopsylla*.

| HOST SPECIES | *C. nidicola* | *C. stanfordi* |
|---|---|---|
| Illinois | | X |
| Indiana | | X |
| Iowa | | X |
| Kansas | X | |
| Maryland | | X |
| Michigan | | X |
| New York | | X |
| Ohio | | X |
| Pennsylvania | | X |
| Utah | | X |
| Wisconsin | | X |
| Ontario | | X |

TABLE 4. Host associations of the genus *Conorhinopsylla*.

| HOST SPECIES | *C. nidicola* | *C. stanfordi* |
|---|---|---|
| *Glaucomys* sp. | | X |
| *Glaucomys sabrinus* | | X |
| *Glaucomys sabrinus macrotis* | | X |
| *Glaucomys volans* | | X |
| *Glaucomys volans volans* | | X |
| *Neotoma* sp. | X | |
| *Neotoma floridana* | X | |
| *Neotoma floridana osagensis* | X | |
| *Peromyscus* sp. | | X |
| *Peromyscus maniculatus* | X | |
| *Procyon lotor* | | X |
| *Sciurus carolinensis* | | X |
| *Sciurus niger* | | X |
| *Spermophilus townsendi* | | X |
| *Tamiasciurus hudsonicus* | | X |
| *Tamiasciurus hudsonicus loquex* | | X |

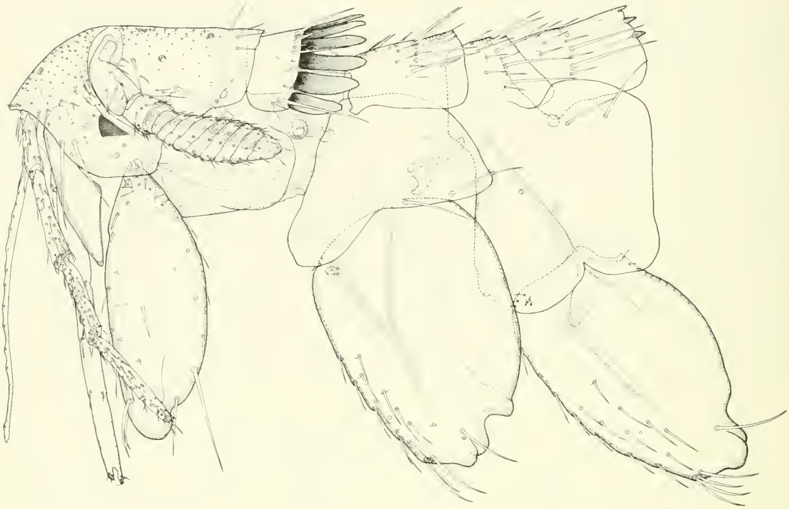


Fig. 15. *Conorhinopsylla stanfordi*; Male, head and thorax including coxae.

### *Conorhinopsylla stanfordi* Stewart
Figs. 15–18, 20, 22, 24, 26, 31

*Conorhinopsylla stanfordi* Stewart 1930:178–179; Jordan 1933:267; Fox 1940:41; Hubbard 1940:37(4); Fuller 1942:137; Jellison and Good 1942:42; Ewing and Fox 1943:74; Fuller 1943:5; Jameson 1943:177; Stanford 1944:174; Jellison 1945:109; Hubbard 1947:102; Jellison, Locker, and Bacon 1953:37; Benton 1955:139–140; Burbutis 1956:782; Layne 1958:162; Geary 1959:355; Stark 1959:97; Benton and Cerwonka 1960:383–391; Hopkins and Rothschild 1962:360; Benton and Smiley 1963:4; Osgood 1964:29–33; Jellison and Glesne 1967:65–66; Benton 1967:150–160; Humphreys 1967:188; Whitaker and Corthum 1967:432; Holland and Benton 1968:256; Tipton and Saunders 1971:18; Amin 1973:110–111; Jenkins and Grundmann 1973:76–86; Haas and Wilson 1973: 302–314; Lewis 1974:147–167; Jackson and Defoliart 1976:351–356.

TYPE HOST.— *Tamiasciurus hudsonicus.*

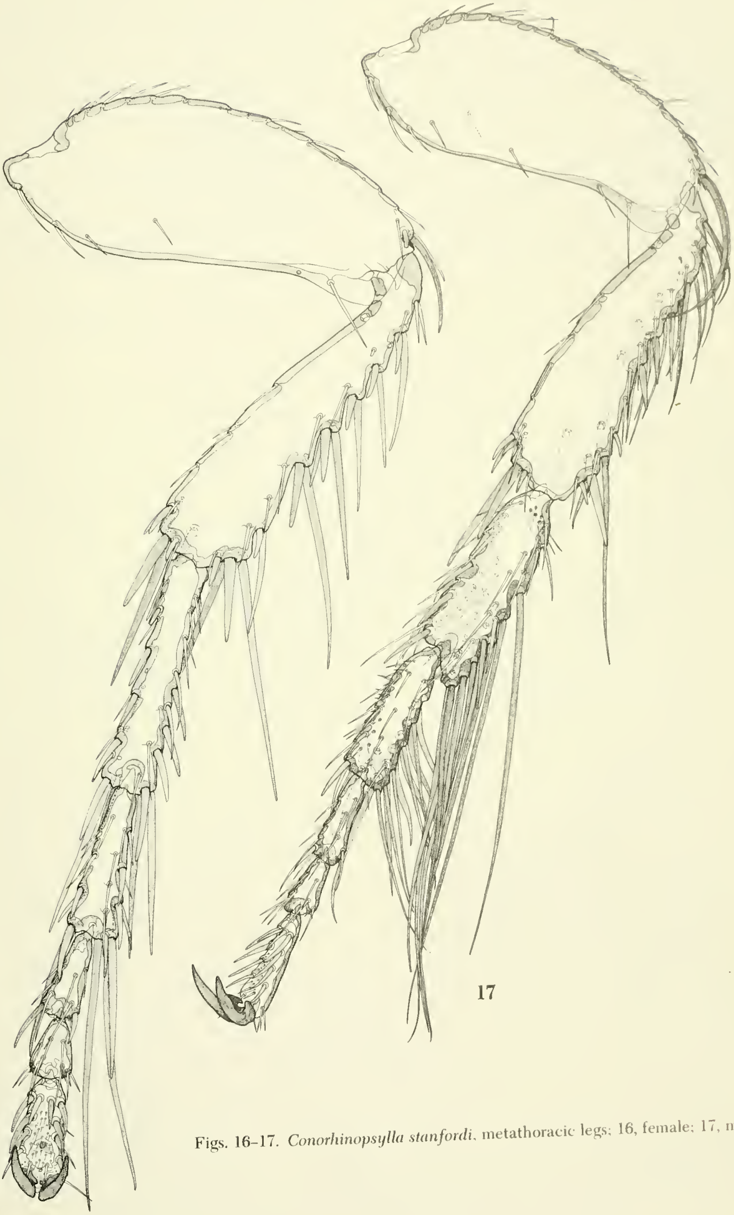
TYPE LOCALITY.— Ithaca, Tompkins Co., New York.

TYPE SPECIMENS.— Collection of M. A. Stewart.

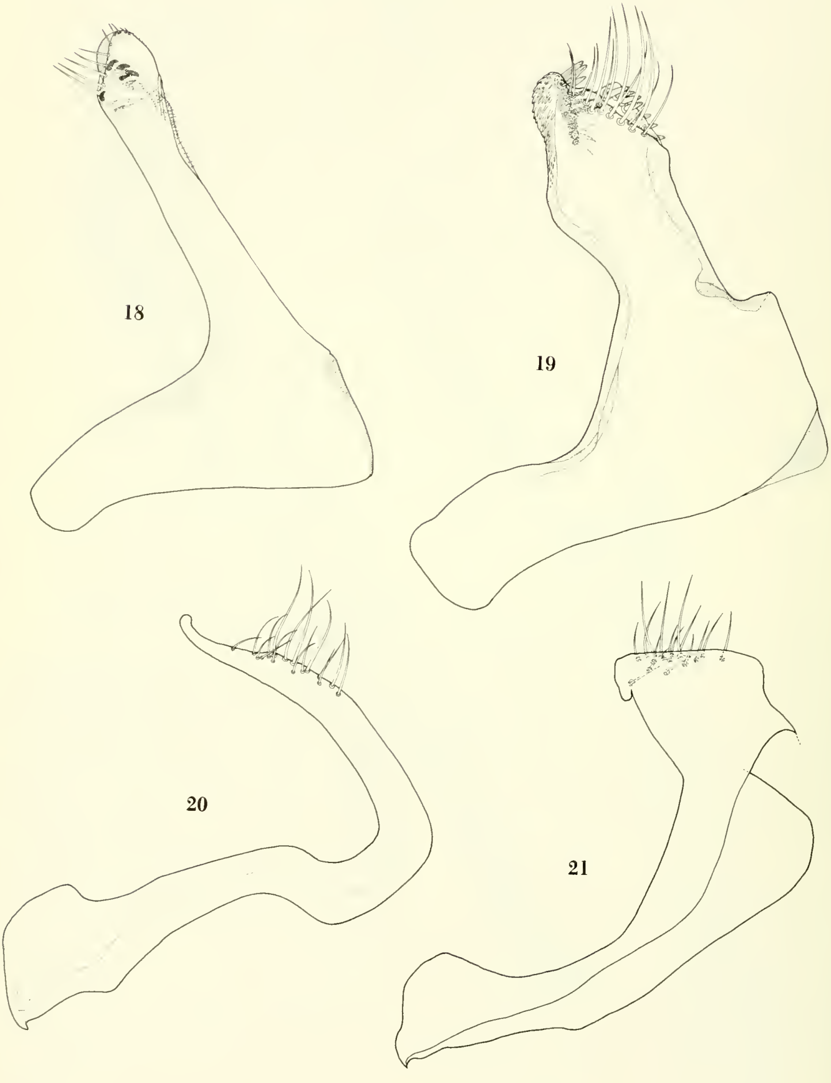
DIAGNOSIS.— *Conorhinopsylla stanfordi* may be distinguished from *C. nidicola*, the only other species in the genus, on the basis of the following set of characters; eye vestigial but sufficiently pigmented to be readily discernible; labial palp with 5–6 segments; in the male the metatibia and first two metatarsal segments with long prominent bristles; clasper projected caudally, fixed and movable processes of clasper about same size; distal arm of sternum VIII narrow but subapical area slightly enlarged and with 4–5 spiniform bristles; the distal arm of sternum IX is narrow, tapers apically and bears several long subapical bristles.

DISTRIBUTION.— ILLINOIS: Madison County. INDIANA: Vigo County. IOWA: Dubuque County. MARYLAND: Frederick County. MICHIGAN: Clinton County. NEW YORK: Otesgo and Ulster counties. OHIO: Athens and Jackson counties. PENNSYLVANIA: Bradford and Erie counties. UTAH: Sevier County. WISCONSIN: Adams and Iowa counties. CANADA: Ontario.

MATERIAL EXAMINED.— MARYLAND: (Frederick Co.) 1 ♂ ex *Tamiasciurus hudsonicus loquex* (nest), 1.5 miles N Wolfsville, 28-XI to 3-XII-1970, Traub and Schlitter; 1 ♀ ex *Glaucomys v. volans*, same collection data;



Figs. 16–17. *Conorhinopsylla stanfordi*, metathoracic legs; 16, female; 17, male.



Figs. 18–21. Males, sternum VIII; 18, *Conorhinopsylla stanfordi*; 19, *C. nidicola*; 20–31. sternum IX; 20, *C. stanfordi*; 21, *C. nidicola*.

1 ♀ ex *Sciurus carolinensis*, Oxon Hill, 5-XII-1923, E. Chapin. OHIO: (Athens Co.) 1 ♂ ex nest of flying squirrel, Waterloo Twp., 10-X-1964, H. G. Humphreys. NEW YORK: (Chautauqua Co.) 1 ♂ ex nest of *Glaucomys volans*, 1 mile S Fredonia; (Otesga Co.) 1 ♂, 1 ♀ ex *Glaucomys volans*, Middlefield Twp., 6-XII-1956, P. Connor.

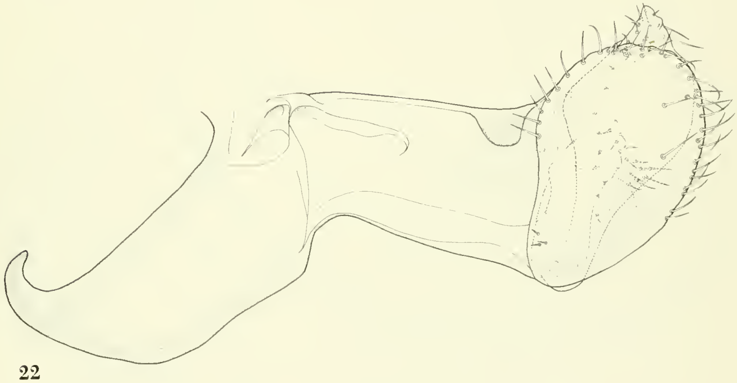
DISCUSSION.— Stanford (1944) reported *C. stanfordi* from Utah but this record is very likely in error. If so, then it can be said that *C. stanfordi* occurs on arboreal squirrels east of the Mississippi River.

### *Conorhinopsylla nidicola* (Jellison)

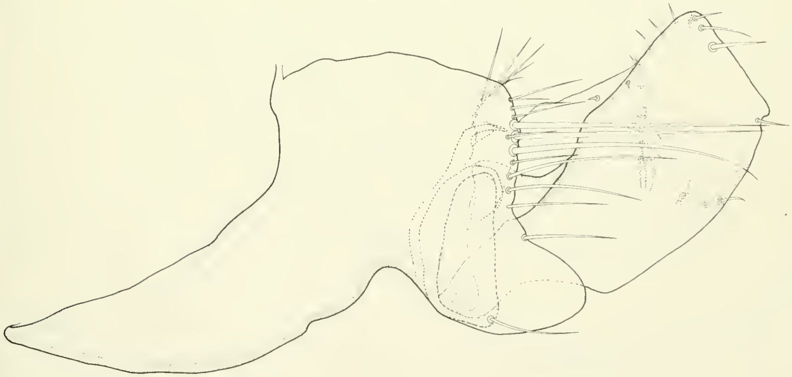
Figs. 19, 21, 23, 25, 27, 31

*Conorhinopsylla nidicola* Jellison 1945:109; Holland 1949b:102; Jellison, Locker, and Bacon 1953:37; Rainey 1956:535–646; Poorbaugh and Gier 1961:201; Hopkins and Rothschild 1962:362; Jellison and Glesne 1967:65; Lewis 1974:147–167.

DIAGNOSIS.— *Conorhinopsylla nidicola* may be characterized as follows: eye vestigial and not readily discernible; labial palp with 8 or more segments; in the male there is no comb-like row of bristles on the hind tibia, and the tarsal bristles are not so long as in *C. stan-*

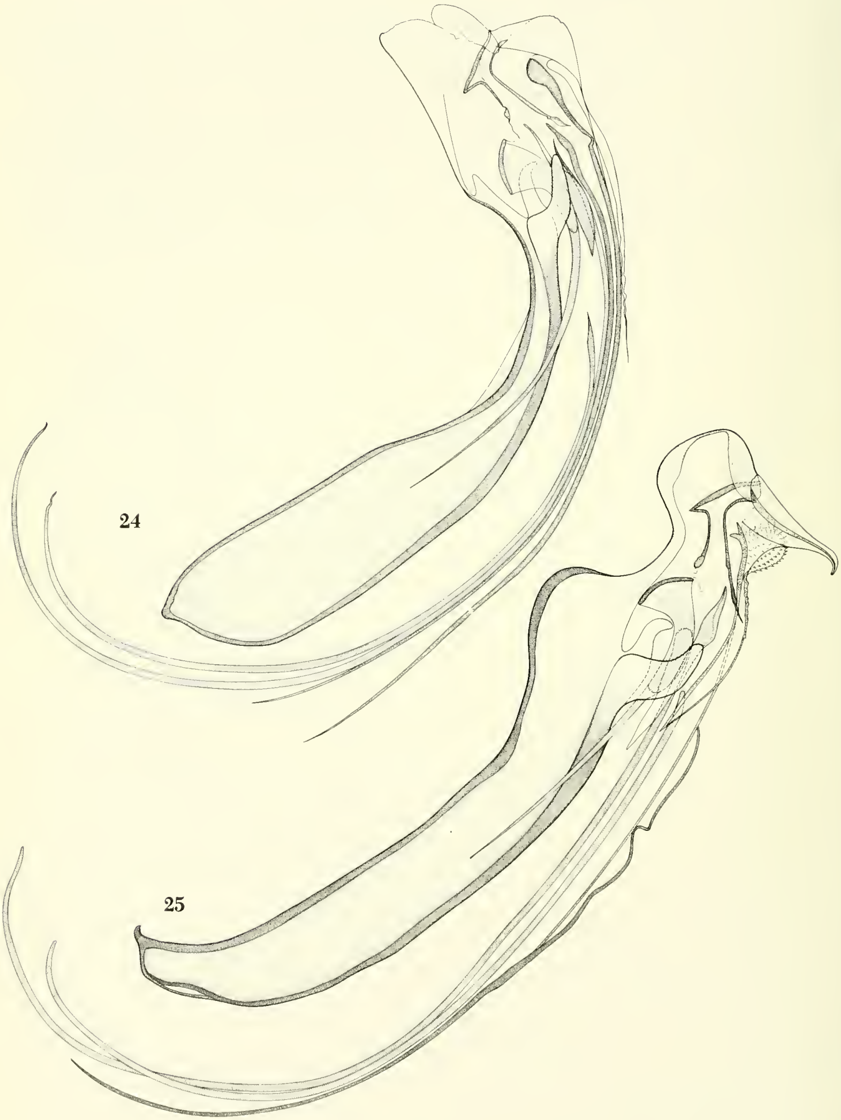


22



23

Figs. 22–23. Males, claspers; 22, *Conorhinopsylla stanfordi*; 23, *C. nidicola*.



Figs. 24–25. Males, aedeagus; 24, *Conorhinopsylla stanfordi*; 25, *C. nidocola*.

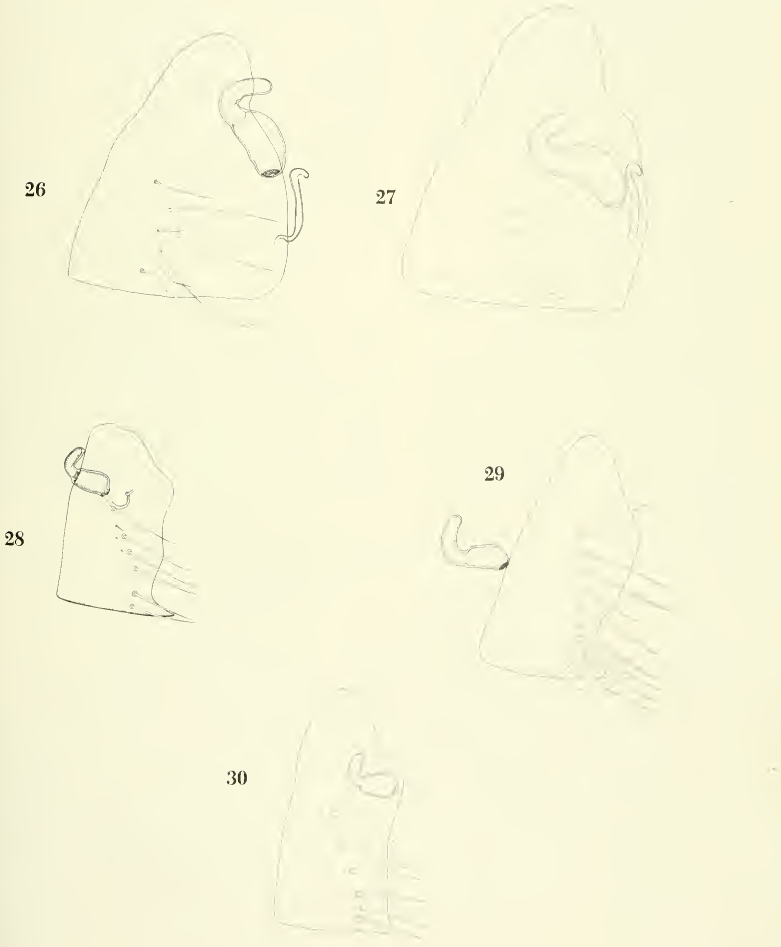
*fordi*; there is no caudal projection of the male clasper and the movable process of the clasper extends dorsally far beyond the fixed process of the clasper; the distal arm of sternum VIII is broad and with 8–10 apical and subapical bristles; the distal arm of sternum IX is broad and with a truncate apex and several marginal and submarginal bristles.

Female characters are not sufficiently distinctive to be diagnostic.

TYPE HOST.— *Neotoma floridana.*

TYPE LOCALITY.— Lawrence, Douglas Co., Kansas.

TYPE SPECIMENS.— Snow Collection, University of Kansas and U.S. National Museum.



Figs. 26–30. Females, sternum VIII; 26, *Conorhinopsylla stanfordi*; 27, *C. nidicola*; 28, *Stenistomera hubbardi*; 29, *S. macrodactyla*; 30, *S. alpina*.

DISTRIBUTION.— KANSAS: Douglas, Riley, and Republic counties.

MATERIAL EXAMINED.— KANSAS: (Douglas Co.), 3♂, 3♀ (paratypes) ex nest of *Neotoma* sp., Lawrence, 11-XI-1944, R. H. Beamer; 2♂ ex *Neotoma* sp., 1959, A. El-Wailly; 1♀ ex *Neotoma floridana*, 1959, A. El-Wailly; 1♀ ex nest of *Neotoma* sp., Lawrence, 10-V-1948, C. E. Hopla; 1♀ ex nest of *Neotoma floridana osagenis*, Lawrence, 13-XII-1947,

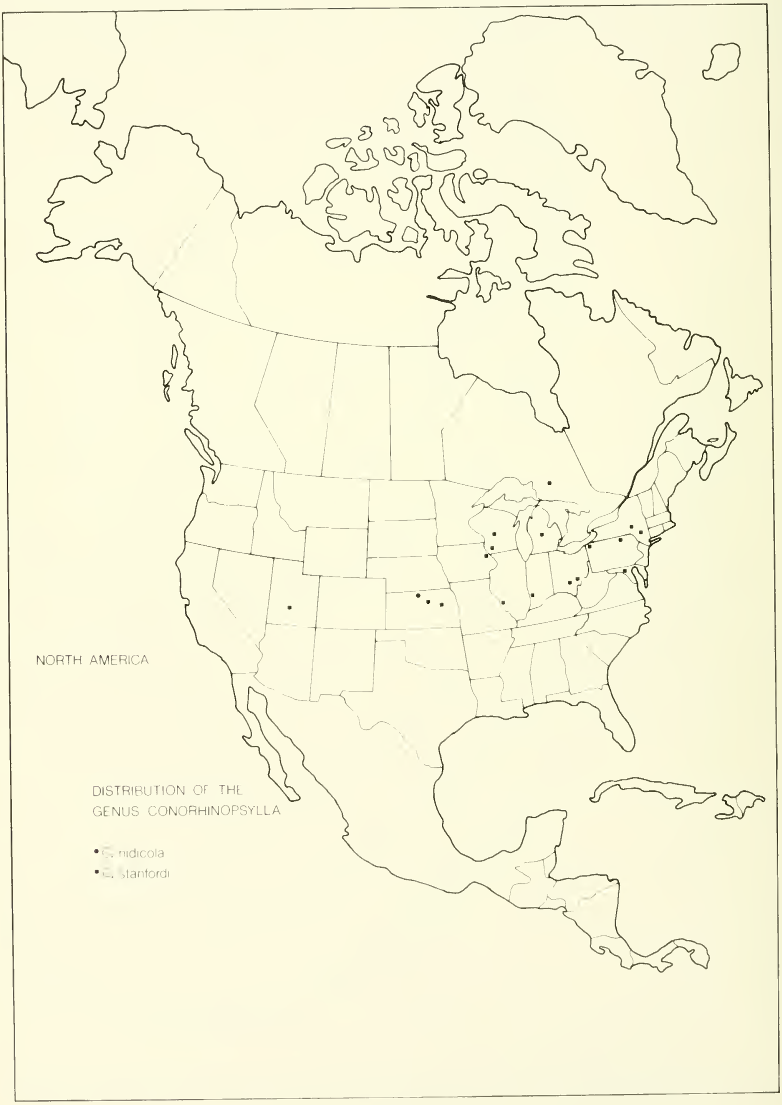

NORTH AMERICA
DISTRIBUTION OF THE
GENUS CONORHINOPSYLLA
• C. nidicola
▪ C. stanfordi

Fig. 31. Distribution of *Conorhinopsylla nidicola* and *C. stanfordi*.

C. E. Hopla; 1 ♂ ex *Neotoma floridana*, Lawrence, 3-XII-1949, C. E. Hopla; 1 ♂, 1 ♀ ex nest of *Neotoma* sp., Lawrence, 30-IX-1948, C. E. Hopla; 1 ♀ ex nest of *Neotoma floridana osagensis*, 22-XI-1952, D. A. Crossley.

DISCUSSION.— *Conorhinopsylla nidicola* is associated with *Neotoma floridana* west of the Mississippi River in Kansas.

### *Megarthroglossus* Jordan & Rothschild

*Megarthroglossus* Jordan and Rothschild 1915:46 (Type species: *Megarthroglossus procus* Jordan and Rothschild, 1915); Ewing 1929:162; Jellison and Good, 1942:83; Ewing and Fox, 1943:113; Hubbard 1947:296; Holland 1949:89; Eads 1950:53–54; Traub and Tipton 1951:267–278; Jellison, Locker, and Bacon 1953:104; Traub 1953:77–85; Morlan 1954:446; Mendez 1956: 159–192; Hopkins 1957:64–67; Finley 1958:213–552; Parker and Howell 1959:597–604; Stark 1959:98; Hopkins and Rothschild 1962:365; Holland 1965:1052; Jellison and Glesne 1967:16; Stark and Kinney 1969:287–294; Mendez and Haas 1972:285–288; Lewis 1974:155; Nelson and Smith 1976:54; Egoscue 1976:475–480.

The Nearctic genus *Megarthroglossus* was established by Jordan and Rothschild in 1915 with *Megarthroglossus procus* as the type species. Baker (1895) described *Pulex longispinus*, which was subsequently placed in the genus *Ceratophyllus* by Wagner (1898) and in the genus *Megarthroglossus* by Jordan and Rothschild (1915). Mendez (1956) revised *Megarthroglossus* and included 12 species and 1 subspecies. Since this revision an additional 3 species have been described: *M. cavernicolus* Mendez and Haas, 1972; *M. wilsoni* Mendez and Haas, 1973; and *M. weaveri* Eads and Campos, 1977. *Megarthroglossus muiri* was reduced to a subspecies of *M. procus* by Hopkins and Rothschild (1962), and we have chosen to retain the two subspecies as valid taxa even though they are very similar morphologically. In this paper *M. pygmaeus* (Wagner 1936) is considered a junior synonym of *M. spenceri*, and *M. divisus exsecatus* is reduced to a junior synonym of *M. divisus*. As a result of these taxonomic changes, the genus *Megarthroglossus* includes 13 known taxa, of which one is a subspecies.

The genus *Megarthroglossus* has been collected in a variety of habitats and from many hosts (Table 6). Species of the genus *Neotoma* appear to be preferred hosts. Species of the genera *Eutamias*, *Glaucomys*, *Ochotona*, *Peromyscus*, and *Tamiasciurus* are considered to be secondary hosts.

The geographical distribution of species and subspecies of *Megarthroglossus* is given in Table 5 and Figures 100, 101. Specimens have been collected from Texas to Canada and from California east to Nebraska.

DIAGNOSIS.— *Megarthroglossus* may be separated from *Callistopsyllus* and *Anomiop-*

TABLE 5. Distribution of species and subspecies of *Megarthroglossus*.

| TAXA | Arizona | California | Colorado | Idaho | Montana | Nebraska | Nevada | New Mexico | Oregon | Texas | Utah | Washington | Wyoming | Alberta | British Columbia |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *M. becki* | | | | | | | | | | | X | | | | |
| *M. bisetis* | | | | | | | | X | | X | | | | | |
| *M. cavernicolus* | | | | | | | | X | | | | | | | |
| *M. divisus* | X | X | X | X | X | X | | X | X | X | X | | X | X | X |
| *M. jamesoni* | | X | | | | | X | | | | | | | | |
| *M. procus muiri* | | X | | | | | | | | | | | | | |
| *M. procus procus* | | X | X | | | X | X | | X | | X | X | X | | X |
| *M. sicamus* | | | | | | | | | | | | | | | X |
| *M. sierrae* | X | | | | | | | | | | | | | | |
| *M. smiti* | | | | | | | X | | | | X | | | | |
| *M. spenceri* | | X | | | | | | | | | | | | | X |
| *M. weaveri* | | | X | | | | | | | | | | | | |
| *M. wilsoni* | | | X | | | | | X | | | | | | | |

*syllus* on the basis of long labial palpi which extend beyond the procoxa and trochanter. *Conorhinopsylla* and *Stenistomera*, the remaining North American genera of the subfamily Anomiopsyllinae, like *Megarthroglossus*, possess long labial palpi, but, unlike *Megarthroglossus*, they have spiniforms on the male genitalia.

DESCRIPTION.— HEAD: Anterior margin of head evenly convex in females; more elongate in males, anterior margin convex to subangulate. Frontal tubercle (clypeus) present, small, inconspicuous. Eye present, reduced, lightly pigmented. Maxillary lobe acuminate to subacuminate, normally not extending beyond middle of second segment of labial palp. Maxillary palp 4-segmented. Labial palp 5-segmented and extends one-half to one full segment beyond procoxa. Trabeculum centralis absent. Genal lobe evenly convex. Genal comb absent. Occular bristle in row of 4 alternating long and short, proceeding from eye to genal margin. Preoccular bristles 0–4, (usually in row of 3), directly over cibarial pump. Posterior antennal fossae with 2 long plus several minute bristles. Antennal fossae prolonged in males, may or may not extend to vertex, to form

TABLE 6. Host associations of the genus *Megarthroglossus*.

| HOSTS | *M. becki* | *M. bisetis* | *M. cavernicolus* | *M. divisus* | *M. jamesoni* | *M. procus muiri* | *M. procus procus* | *M. sicamus* | *M. sierrae* | *M. smiti* | *M. spenceri* | *M. weaveri* | *M. wilsoni* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ammospermophilus leucurus leucurus* | | | | | | | | | | | X | | |
| *Canis latrans* | | | | | | | | X | | | | | |
| "Chipmunk" | | | | | | | X | | | | | | |
| *Dipodomys spectabilis* | | X | | | | | | | | | | | |
| *Eutamias* sp. | | | | | | | | | | | | | X |
| *Eutamias minimus* | | | | | | | | | | | | | X |
| *Eutamias quadrivittatus* | | | | | | | X | | | | | | |
| *Eutamias townsendi* | | | | | | | X | | | | | | |
| *Glaucomys* sp. and nest | | | | X | | | X | | | | | | |
| *Glaucomys sabrinus* | | | | | | | X | | | | | | |
| *Glaucomys s. lascivus* | | | | | | | X | | | | | | |
| *Glaucomys s. oregonesis* | | | | | | | X | | | | | | |
| *Lynx* sp. | | | | | | | | X | | | | | |
| *Microtus longicaudus* | | X | | | | | | | | | | | |
| "Mouse" | | | | X | | | | | | | | | |
| *Neotoma* sp. and nest | | X | | X | | | X | | | | | | |
| *Neotoma albigula* and nest | X | X | | X | | | | | | | | | |
| *Neotoma cinerea* and nest | X | X | X | X | X | | X | | | | X | | |
| *Neotoma c. acraia* | X | | | | | | | | | | | | |
| *Neotoma c. cinerea* | | | | X | | | | | | | | | |
| *Neotoma c. occidentalis* | | | | | | | X | X | | | | | |
| *Neotoma lepida* | | | | X | | | | | | X | | | |
| *Neotoma l. lepida* | | | | | | | | | | X | | | |
| *Neotoma mexicana* | | X | | | | | | | | | | X | |
| *Neotoma micropus* | | X | | | | | | | | | | | |
| *Neotoma m. canescens* | | X | | | | | | | | | | | |
| *Onychomys leucogaster* | | X | | | | | | | | | | | |

falx. Tentorial arch present, well developed, located anterior to eye.

THORAX: Prosternum with dorsal angulate to subangulate inflexion at posterior one-third of ventral margin. Pronotal comb present, 6 to 8 blunt, broad spines per side. Thoracic link plates II and III well developed. Mesonotum with 3 distinct rows of bristles. Mesepimeron usually with 3 long bristles, anteriormost close to or directly over pleural rod. Mesepisternum with row of small bristles, extending from dorsal angle to mid-segment. Metanotum with one row bristles. Lateral metanotal area not complete, sclerites partially fused. Metepisternum partly fused with metasternum and metepimeron to metanotum; setation sparse, normally with 3 long bristles, one near caudal margin, 2 in proximity to pleural rod.

LEGS: Profemur with 2–3 lateral bristles on mesal surface. Metatarsus II with 1–2 long, lateral, apical bristle(s), extending from one-half to full length of metatarsus V. Metatarsus V with 4 pairs lateral plantar bristles, 1 basoventral pair.

ABDOMEN: Abdominal tergal spinelets variable, generally tergum I with 1–2, tergum II with one per side. Abdominal terga with one

Table 6 continued.

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ochotona* sp. | | | | | | | | | X | | | | |
| *Ochotona princeps* | X | X | | X | | | X | | | | X | | |
| *Ochotona schisticeps* | | | | | | X | | | | | | | |
| *Ochotona muiri* | | | | | | | | | X | | | | |
| *Peromyscus* sp. | | X | | X | | | | | | | | | X |
| *Peromyscus boylii* | | X | | X | | | X | | | | | | |
| *Peromyscus crinitus pergracilis* | | | | | | | | | | X | | | |
| *Peromyscus leucopus* | | X | | X | | | | | | | | | |
| *Peromyscus maniculatus* | | | | X | | | X | | | | | | X |
| *Peromyscus m. rubidus* | | | | | | | X | | | | | | |
| *Peromyscus m. sonoriensis* | | | | X | | | | | | X | | | |
| *Peromyscus nasutus* | | X | | | | | | | | | | | |
| *Peromyscus truei* | | X | | X | | | X | | | | | | |
| *Peromyscus t. nevadensis* | | | | X | | | | | | X | | | |
| *Rattus norvegicus* | | | | | | | X | | | | | | |
| *Sigmodon hispidus* | | X | | | | | | | | | | | |
| *Sorex palustris navigator* | | | | | | X | | | | | | | |
| *Spilogale* sp. | | | | | | | | X | | | | | |
| *Spilogale gracilis saxatilis* | | | | | | | | | | X | | | |
| *Sylvilagus nuttallii* | | X | | | | | | | | | | | |
| *Tamiasciurus* sp. and nest | | | | X | | | X | | | | | | |
| *Tamiasciurus hudsonicus* | | X | | X | | | | | | | | | |
| *Tamiasciurus h. douglasi* | | | | X | | X | X | | | | | | |
| *Tamiasciurus h. albolimbatus* | | | | | | | X | | X | | | | |
| *Tamiasciurus h. fremonti* | | | | X | | | | | | | | | |
| *Tamiasciurus h. streatori* | | | | X | | | | | | | | | |
| *Thomomys bottae* | X | | | | | | | | | | | | |
| *Thomomys talpoides* | | X | | | | | | | | | | | |
| "Weasle" | | | | X | | | | | | | | | |

row of 5–7 long bristles intermixed with several minute bristles, ventralmost long bristle shifted anterad of main row of bristle. Lateral bristles on abdominal sterna variable, usually in row of 2–4 per side. Antepygidial bristles 2–3 depending on species: those with 3, centermost longest with upper and lower varying from minute to small (in males) or from two-thirds to three-fourths length of center bristle (in females); those with 2, uppermost longest with lower varying from minute to medium (in males), three-fourths to almost as long as upper (in females).

*Modified segments—Male*: Fixed process of clasper with hump (inner fovea), one-half distance from acetabular area to apex of process, may be marginal or submarginal. Caudal margin of fixed process with 2–3 (usually 3) long, stout bristles dorsad of acetabular area, one bristle ventrad to acetabular area. Shape of caudal margin of sternum VIII variable, diagnostic in some species, normally ensheathing distal one-half to two-thirds of distal arm of sternum IX. Proximal arm of sternum IX expanded, with or without cephalad-directed projection. Shape of distal arm of sternum IX variable, diagnostically distinct in some species. Aedeagal apodeme blade shaped, tapering at neck, without proximal or apical spur. Dorsal margin either straight, with slight undulation, or possessing prominent hump in proximity of crescent sclerite. Median dorsal lobe acuminate, truncate, or broadly convex. Crochet of aedeagus large, conspicuous; caudal border variable; apical process hooklike, rounded, or absent. Apex of sclerotized inner tube truncate, with distinct dorsolateral projection. Satellite sclerite closely associated with sclerotize inner tube. Penis rods uncoiled, extending slightly dorsad of apex of aedeagal apodeme.

*Modified segments—Female*: Caudal margin of sternum VII undulate, sinus present or absent on ventrolateral aspect. Anal stylet variable in length, setation varies according to species. Spermatheca variable, bulga may be elongate or compressed. Hilla bent sharply or gently curved dorsad, distal end varying from narrowly convex or broadly convex to subtruncate.

The genus *Megarthroglossus* is a complex group of closely related species with many similar morphological features. Often the description of one species applies equally well to several other species. For this reason, a detailed description of all species is not given but, instead, a short, narrative diagnosis for each species is presented.

Keys to both males and females (except for the female of *M. sicamus*) are given. It should be emphasized that overlap between species was observed for several taxonomic characters. Characters used in the key include measurements whenever possible with the intent of excluding such ambiguous terms as *prominent*, *not deeply indented*, and *narrow*, to mention but a few. In addition, the key to the females may not be entirely satisfactory, but it is intended to fill a void because current literature does not include keys to the females. *Megarthroglossus sicamus* is not included in the key because specimens were not available. If *M. sicamus* were included in the key, it would be placed near *M. jamesoni* and *M. cavernicolus*.

## Key to Species of *Megarthroglossus* (Males)

| | | |
|---|---|---|
| 1. | Height of hump on dorsal margin of aedeagus greater than 10 microns | 2 |
| — | Hump of dorsal margin of aedeagus absent, or, if present, height less than 10 microns | 6 |
| 2(1). | Posterior margin of sternum VIII evenly convex; inner fovea of immovable process more than 60 microns below dorsal margin; hump on dorsal margin of aedeagus exceeds 30 microns | *sicamus* |
| — | Posterior margin of sternum VIII sinuate; inner fovae of immovable process less than 60 microns below dorsal margin (Fig. 32); hump on dorsal margin of aedeagus variable | 3 |

3(2). Anterior margin of finger of clasper with angular denticle; hump on dorsal margin of aedeagus exceeds 20 microns; inner fovea of immovable process exceed 50 microns below dorsal margin; ventrolateral lobe of sternum VIII evenly convex ........ *spenceri*

— Anterior margin of finger of clasper without angular denticle; inner fovea of immovable process less than 50 microns below dorsal margin; ventrolateral lobe of sternum VIII variable ........ 4

4(3). Median dorsal lobe of aedeagus reduced to short, blunt lobe; posterior margin of sternum VIII sinuate, with truncate to subtruncate ventrolateral lobe ........ 5

— Median dorsal lobe of aedeagus long, with curved apex; posterior margin of sternum VIII undulate, with a short subacuminate lobe ........ *smiti*

5(4). Hump on dorsal margin of aedeagus less than 20 microns; length of labial palp segment V less than 220 microns; inner fovea of immovable process exceeds 30 microns, marginal; ventrolateral lobe of sternum VIII subtruncate ........ *sierrae*

— Hump on dorsal margin of aedeagus exceeds 30 microns; length of labial palp segment V exceeds 220 microns; inner fovea of immovable process exceeds 30 microns, submarginal; ventrolateral lobe of sternum VIII truncate ........ *jamesoni*

6(1). Ventrolateral lobe of sternum VIII long, fingerlike, curved ventrad; inner fovea of immovable process exceeds 50 microns, marginal ........ *becki*

— Ventrolateral lobe of sternum VIII not fingerlike; posterior margin of sternum VIII variable; inner fovea of immovable process less than 50 microns, submarginal ........ 7

7(6). Posterior margin of sternum VIII evenly convex; 2 or 3 antepygidial bristles ........ 8

— Posterior margin of sternum VIII sinuate, with variable shaped ventrolateral lobe; 3 antepygidial bristles ........ 9

8(7). Two or 3 antepygidial bristles per side; inner fovea of immovable process less than 35 microns; segment V of labial palp less than 220 microns in length; crochet spur exceeds 10 microns in length; finger of clasper less than 120 microns in length; metatarsal segment I less than 220 microns in length ........ *bisetis*

— 2 antepygidial bristles per side; inner fovea of immovable process exceeds 35 microns; segment V of labial palp exceeds 220 microns in length; crochet spur less than 10 microns in length; finger of clasper exceeds 120 microns in length ........ *weaveri*

9(7). Ventrolateral lobe of sternum VIII divided into upper convex lobe and lower acuminate lobe; crochet spur less than 10 microns in length ........ 10

— Ventrolateral lobe of sternum VIII not divided; crochet spur exceeds 10 microns in length ........ 11

10(9). Width of median dorsal lobe of aedeagus exceeds 20 microns; segment V of labial palp exceeds 140 microns in length; depth of sinus in sternum VIII less than 45 microns ........ *procus procus*

— Width of median dorsal lobe of aedeagus less than 20 microns; segment V of labial palp less than 130 microns in length; depth of sinus in sternum VIII exceeds 45 microns ........ *procus muiri*

11(9). Inner fovea of immovable process less than 20 microns below the dorsal margin; crochet spur less than 20 microns in length; sternum IX less than 180 microns in length ........ *cavernicolus*

— Inner fovea of immovable process more than 25 microns from dorsal margin; crochet spur exceeds 30 microns in length; sternum IX exceeds 180 microns in length ........ 12

12(11). Inner fovea of immovable process less than 20 microns in length; crochet spur less than 60 microns in length; segment V of labial palp more than 170 microns in length ........ *divisus*

— Inner fovea of immovable process exceeds 40 microns in length; crochet spur exceeds 60 microns in length; segment V of labial palp less than 170 microns in length ........ *wilsoni*

### Key to Species of *Megarthroglossus* (Females)

1. Bulga of spermatheca compressed (i.e., appears to be withdrawn into itself (Fig. 86) ........ 5

— Bulga of spermatheca not compressed (Fig. 84) ........ 2

2(1). Posterior margin of sternum VII with sinus ........ 3

— Posterior margin of sternum VII without sinus ........ 4

3(2). With 3 antepygidial bristles per side; segment V of labial palp less than 300 microns in length; hilla of spermatheca less than 40 microns in width (Fig. 94) . *spenceri*

— With 2 antepygidial bristles per side; segment V of labial palp exceeds 300 microns in length; hilla of spermatheca more than 40 microns in width ........ *weaveri*

4(2). With 3 or 4 antepygidial bristles per side; pronotal comb with 7–8 spines per side; segment V of labial palp less than 230 microns in length; hilla of spermatheca less than 40 microns in width ........ *cavernicolus*

— With 3 antepygidial bristles per side; pronotal comb with 8–9 spines per side; segment V of labial palp more than 270 microns in length; hilla of spermatheca more than 40 microns in width ........ *jamesoni*

5(1). Posterior margin of sternum VII with sinus, more than 10 microns in depth (Fig. 33) ........ 8

— Posterior margin of sternum VII usually without sinus but if present then less than 10 microns in depth ........ 6

6(5). Distal portion of hilla of spermatheca more than 115 microns, more than 50 microns in width; metatarsal segment I more than 300 microns in length ........ *sierrae*

— Distal portion of hilla of spermatheca less than 114 microns, less than 50 microns in width; metatarsal segment I less than 290 microns in length ........ 7

7(6). With 3 antepygidial bristles; pronotal comb with 6 spines per side; spermathecal hilla ratio (vertical length: horizontal length) exceeds 1.50; spermathecal bulga ratio (width of bulga at point of greatest width; width of bulga at point of narrowest width) exceeds 1.50. (Fig. 34) ........ *procus muiri*

— With 2–3 antepygidial bristles: pronotal comb with 6–8 spines per side; spermathecal hilla ratio less than 1.20; spermathecal bulga ratio less than 1.40 ........ *procus procus*

8(5). Hilla of spermatheca more than 40 microns in width; sternum VII sinus depth to width ratio less than 2.00; with 2 antepygidial bristles per side; pronotal comb with 8 spines per side; spermathecal hilla ratio less than 1.10 with bulga ratio exceeds 1.50 ........ *bisetis*

— Hilla of spermatheca less than 40 microns in width; sternum VII sinus depth to width ratio exceeds 2.00; antepygidial bristles variable, 1–4 per side; pronotal comb spines variable, 6–8 per side; spermathecal hilla exceeds 1.10 with bulga ratio exceeds 1.70 (if hilla ratio less than 1.10, then bulga ratio less than 1.50) ... ........................................ 9

9(8). Sternum VII sinus depth to width ratio exceeds 2.40; with 2–4 antepygidial bristles per side; pronotal comb with 6–8 spines per side; segment V of labial palp exceeds 270 microns in length (average) ........................................ 10

— Sternum VII sinus depth to width ratio less than 2.40; with 3 antepygidial bristles per side; pronotal comb with 7–8 spines per side; segment V of labial palp less than 270 microns in length (average) ........................................ 11

10(9). Sternum VII sinus ratio exceeds 4.00; spermathecal hilla ratio exceeds 1.20 and bulga ratio exceeds 1.80; pronotal comb with 8 spines per side .................... *smiti*

— Sternum VII sinus ratio less than 3.00; spermathecal hilla ratio less than 1.20 and bulga ratio less than 1.70; pronotal comb with 6–8 spines per side ........... *divisus*

11(9). Pronotal comb with 8 spines per side; spermathecal hilla width exceeds 35 microns; segment V of labial palp more than 260 microns in length; spermathecal hilla ratio less than 1.10 and bulga ratio less than 1.50 ........................................ *becki*

— Pronotal comb with 7 spines per side; spermathecal hilla width less than 35 microns; segment V of labial palp less than 260 microns in length; spermathecal hilla ratio exceeds 1.20 and bulga ratio exceeds 1.80 ........................................ *wilsoni*

Mendez (1956) pointed out that many of the morphological characters of the female are variable and unreliable; therefore, he did not include a key to the females in his paper. It is important to consider the following when using the above key for females: (1) Definitive determination of the female should be based on presence of the male. (2) The key is useful if *only* females are collected. (3) The key does not include *Megarthroglossus sicamus* because a specimen was not available to us; however, it would occur in couplet 4 along with *M. cavernicolus* and *M. jamesoni*.

Previous authors have used the phrase (when referring to the posterior margin of sternum VII) "sinus lacking," or "sinus present but shallow." In many instances, the difference between lacking a sinus to having a shallow sinus is only an interpretation of the author. To clarify this point, we have used a comparison of depth to width. A width to depth ratio that exceeds 5 means that the margin has only a slight concavity and appears to lack a well-defined sinus.

## *Megarthroglossus becki* Tipton & Allred

Figs. 35, 37, 40, 42, 68, 82, 100

*Megarthroglossus becki* Tipton and Allred 1951:108, 113; Mendez 1956:166; Stark 1959:100; Parker and Howell 1959:597–604; Hopkins and Rothschild 1962:380; Jellison and Glesne 1967:167; Tipton and Saunders 1971:18; Mendez and Haas 1972:285–288; Mendez and Haas 1973:1132; Lewis 1974:155.

Type host.— *Neotoma cinerea acraia* Nest.

Type locality.— Buckley's Mine, Rock Canyon, Provo, Utah Co., Utah.

Type specimens.— United States National Museum, Washington, D.C.

Diagnosis.— Male: The ventrolateral lobe of sternum VIII has a long, fingerlike caudally curved extension which distinguishes it from all other species (Fig. 40). The inner fovea of the immovable process (Fig. 42) of the clasper is located on the caudal margin and is more than 50 microns below dorsal margin of clasper. The hump on the dorsal margin of the aedeagus varies in height from 4.4 to 11.0 microns (average of 8.0). In most of the specimens measured, the hump was observed as only a slight swelling in the area

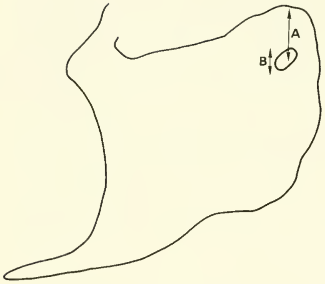


Fig. 32. Measurements which show the position of the inner fovea in relation to the dorsal margin of the immovable process of the clasper. A represents the distance of the fovea from the dorsal margin of the clasper. B represents the length of the inner fovea. The inner fovea in this illustration is submarginal.

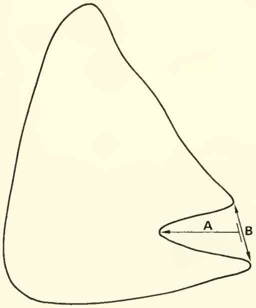


Fig. 33. Measurements of the sinus in the caudal margin of the female sternum VII. A represents the depth of the sinus and B represents the width of the sinus. The sinus ratio is equal to B divided by A.

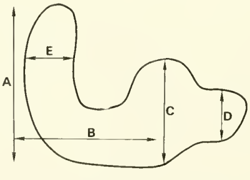


Fig. 34. Measurements of the spermatheca: A over B = hilla ratio; C over D = bulga ratio; E = width of hilla.

of the dorsal margin between the crescent sclerite and the sclerotized inner tube (S.I.T.).

Female: The sinus in the posterior margin of sternum VII is more than 10 microns in depth or the depth to width ratio is less than 2.40 (see Fig. 2). Segment V of the labial palp is less than 270 microns in length (average). *Megarthroglossus becki* can be separated from *M. wilsoni*, its closest relative, in that the hilla is more than 35 microns in width, and it is less than 35 microns in *M. wilsoni*.

Distribution.— Utah: Kane, Piute, Utah, and Wayne counties.

Material examined.— Utah: (Kane Co.) 5♂, 3♀, ex *Neotoma albigula*, 5-XII-1971, BYU; 1♂, ex *Neotoma cinerea*, 13-X-1971, BYU; 1♂, ex *Peromyscus crinitus*, 11-XII-1971, BYU (these three collections were made in the NAV-KAI project site); (Piute Co.) 1♀, ex *Thomomys bottae*, Kingston, 26-VI-1952, Killpack and Beck, BYU; (Utah Co.) 3♂, 7♀ paratypes, ex *Neotoma cinerea* nest, Buckley's Mine, Provo, 24-XI-1949, Allred, BYU; 4♀, same host, same location 21-X-1950, Allred, BYU; 4♂, 4♀, same host, Provo, 25-XI-1948, Tipton, BYU; 1♀, same host, Rock Canyon, Provo, 24-II-1951, Allred and Beck, BYU; 1♀, same host, same location, 30-III-1951. Allred and Beck, BYU; 2♂, 3♀, ex *Neotoma cinerea*, Aspen Grove, American Fork Canyon, American Fork, 13-X-1951, Barnum et al., BYU; 1♂, 19♀, same host, Thistle, 2-XI-1951, Barnum et al., BYU; 3♀, same host, Spanish Fork Canyon, Spanish Fork, 2-XI-1951, Barnum et al., BYU.

Discussion.— This species is associated with *Neotoma cinerea* ssp. and more particularly with the nests of this host. *Neotoma cinerea* occurs in Utah, Idaho, Arizona, Nevada, and California; however, *M. becki* has been collected only in Utah. It is likely that it has a broader distribution than collection records indicate.

### *Megarthroglossus bisetis* Jordan & Rothschild

Figs. 45, 57, 72, 85, 101

*Megarthroglossus bisetis* Jordan and Rothschild 1915:54; Jellison and Good 1942:83; Ewing and Fox 1943:112; Eads and Menzies 1949:33–39; Eads 1950:54; Traub and Hoff 1951:1–23; Williams and Hoff 1951:310–311; Jellison, Locker, and Bacon 1953:104; Morlan 1954:446–448; Morlan 1955:93–125; Mendez 1956:167–168; Hopkins and Rothschild 1962:390; Jellison and Glesne 1967:168; Rail et al. 1969:92–94; Forcum et al. 1969:412; Miller et al. 1970:698, 700–701; Clark et al. 1971:1191; Mendez and Haas 1972:285–288; Mendez and Haas 1973:1132; Lewis 1974:155.

*Megarthroglossus divisus bisetis*: Hubbard 1947:302; Jellison and Senger 1976:79.

TYPE HOST.— *Neotoma* sp.

TYPE LOCALITY.— Beulah, San Miguel Co., New Mexico.

TYPE SPECIMENS.— British Museum of Natural History, South Kensington, London, England.

DIAGNOSIS.— MALE: The posterior margin of sternum VIII is evenly convex and there are 2 or 3 (usually 2) antepygidial bristles as in *M. weaveri*. *Megarthroglossus bisetis* may be separated from *M. weaveri* on the basis of the following characters: the inner fovea of the immovable process is less than 35 microns from the dorsal margin; segment V of labial palp is less than 220 microns in length; the spur of the crochet is more than 10 microns in length; and the finger of the clasper is less than 120 microns in length.

FEMALE: *Megarthroglossus bisetis*, *M. weaveri*, and some specimens of *M. smiti* and *M. divisus* possess two antepygidial bristles. *Megarthroglossus bisetis* may be separated from *M. smiti* and *M. divisus* in that the hilla of the spermatheca exceeds 30 microns in width and sternum VII has a sinus depth-to-width ratio of less than 2.00, whereas this ratio is greater than 2.00 in *M. smiti* and *M. divisus*. *Megarthroglossus bisetis* can be separated from *M. weaveri* in that the former has a bulga which is compressed (the portion of the bulga to which the spermathecal duct attaches appears to be withdrawn or pushed into the other portion of the bulga).

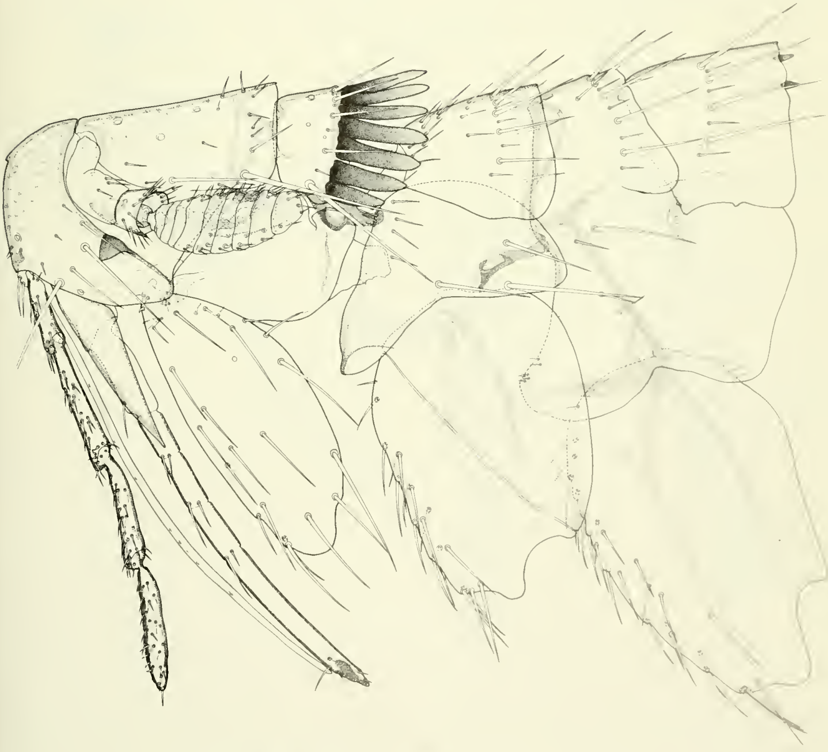
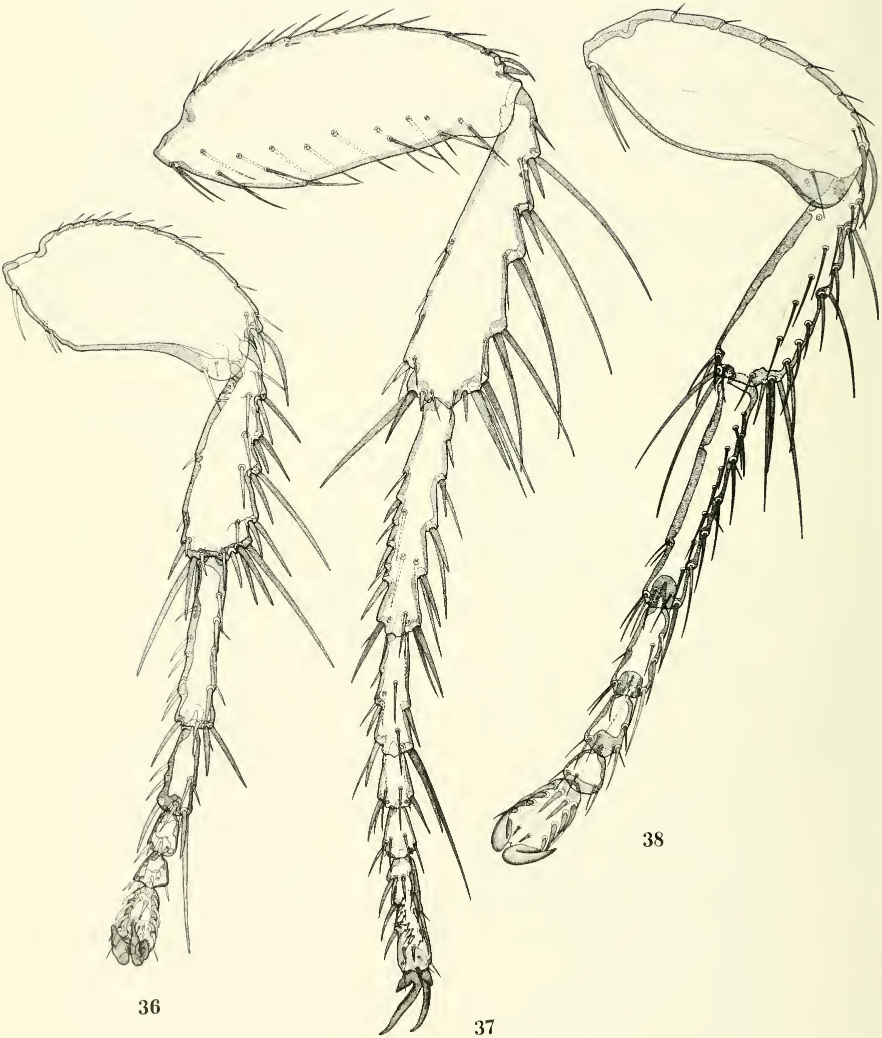


Fig. 35. *Megarthroglossus becki*: Male, head and thorax including coxae.



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Figs. 36–38. Males, metathoracic legs; 36, *Callistopsyllus terinus deuterus*; 37, *Megarthroglossus becki*; 38, *Stenistomera alpina*.

DISTRIBUTION.— NEW MEXICO: Bernalillo, Chaves, Colfax, Guadalupe, Los Alamos, McKinley, Rio Arriba, Sandoval, San Miguel, Santa Fe, and Valencia counties. TEXAS: Donley County. The usual host is *Neotoma*, but a few records are from *Peromyscus*.

MATERIAL EXAMINED.— NEW MEXICO: (Chaves Co.) 5♂, 6♀, ex *Neotoma micropus*, Red Bluff Ranch, 25-V-1967, Miller (Lewis); (McKinley Co.) 1♀, ex *Neotoma mexicana*, Fort Wingate Army Depot, 12-X-1977, Marroquin (USAGHA).

### *Megarthroglossus cavernicolus* Mendez & Haas

Figs. 39, 41, 70, 83, 100

*Megarthroglossus cavernicolus* Mendez and Haas 1972:285–288, 1973:1137.

TYPE HOST.— *Neotoma cinerea* nest.

TYPE LOCALITY.— Jemez Mts., Sandoval Co., New Mexico.

TYPE SPECIMENS.— United States National Museum, Washington, D.C.

DISTRIBUTION.— NEW MEXICO: Sandoval County.

DIAGNOSIS.— MALE: The dorsal margin of the aedeagus is straight or, if a hump is present, its height is less than 7 microns. The inner fovea of the immovable process is less than 20 microns below the dorsal margin of the clasper, and is submarginal in relation to the posterior border. The posterior margin of sternum VIII is sinuate, with a subtruncate ventrolateral lobe. The spur of the crochet is less than 20 microns in length. Sternum IX is less than 180 microns in length. *Megarthroglossus cavernicolus* resembles *M. divisus* and *M. wilsoni*, but the characters given above will serve to separate these species.

FEMALE: The bulga is not compressed in *M. cavernicolus*, *M. weaveri*, *M. spenceri*, and *M. jamesoni*. *Megarthroglossus weaveri* and *M. spenceri* possess a sinus in the posterior margin of sternum VII, which is lacking in *M. cavernicolus* and *M. jamesoni*. *Megarthroglossus cavernicolus* can be separated from *M. jamesoni* in that segment V of the labial palp is less than 230 microns in length and the hilla is less than 40 microns in width. Also, *M. cavernicolus* could be confused with *M. sicamus*; however, the hilla of *M. sicamus* is curved toward the bulga instead of bent away from the bulga as in *M. cavernicolus*.

DISTRIBUTION.— NEW MEXICO: Sandoval County.

MATERIAL EXAMINED.— NEW MEXICO: (Sandoval Co.) 11♂, 21♀ paratypes, ex *Neotoma cinerea* nest, cave west edge Valle Grande, Jemez Mts., 2636 m, 18-IX-1970, Haas et al. (Mendez); 1 paratype ♀, ex *Neotoma cinerea* nest, cave northwest side Telephone Canyon, Jemez Mts., 2600 m, 20-XI-1970, Haas et al. (Mendez).

DISCUSSION.— *Megarthroglossus cavernicolus* and *M. bisetis* have been collected from the same wood rat nest. Further study is necessary to understand more fully the ecological and taxonomic relationships of these two species. Mendez (1956) indicated that *M. cavernicolus* may be sympatric with *M. divisus* as well. *Neotoma cinerea* appears to be the preferred host for this flea.

### *Megarthroglossus divisus* (Baker)

Figs. 47, 48, 59, 60, 73, 74, 86, 87, 100

*Pulex divisus* Baker 1889:54

*Ceratophyllus divisus* Baker 1904:388, 441; Baker 1905:134; C. Fox 1914:27; Dunn and Parker 1923:2772, 2775.

*Ceratophyllus longispinus* Wagner 1889:560.

*Pulex longispinus*: Baker 1895:131–132.

*Megarthroglossus longispinus*: Jordan and Rothschild 1915:52–53; Wagner 1930:130; Wagner 1936:186; Spencer 1936:14; Eskey and Haas 1939:1472; Mail and Holland 1939:126; Eskey and Haas 1940:29–74.

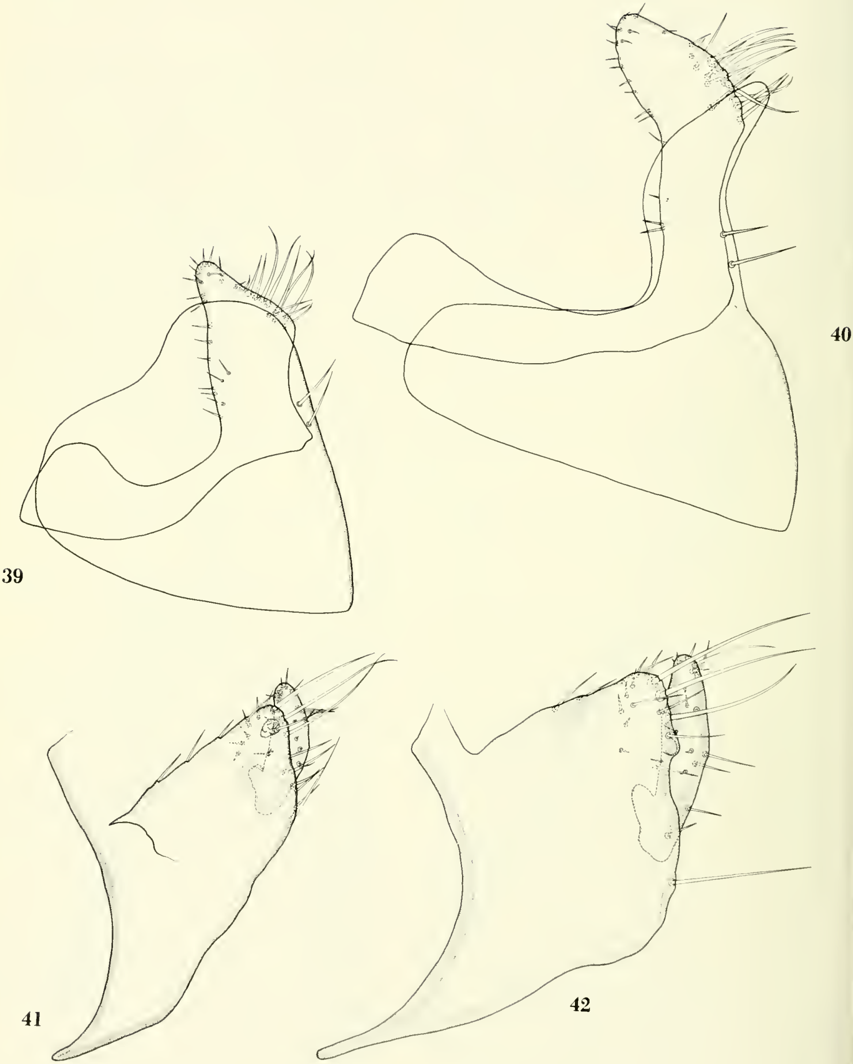
*Megarthroglossus longispinus* var. *exsecatus* Wagner 1936:196.

*Megarthroglossus divisus*: Spencer 1936:14; Hubbard 1940:37(4); Auguston 1941:1952; Jellison, Kohls, and Mills 1943:1–22; Stanford 1944:175; Brown 1944:209; Pollitzer 1952:231–342; Allred 1968:73–87; Mendez and Haas 1972:285–288; Jellison and Senger 1976:79.

*Megarthroglossus divisus* (*longispinus*) var. *exsecatus*: Holland 1949a:11.

*Megarthroglossus divisus exsecatus*: Jellison and Good 1942:83; Ewing and Fox 1943:112–113; Hubbard 1943: 1–12; Hubbard 1947:301; Holland 1949a:9; Holland 1949b:99–100; Jellison, Locker, and Bacon 1953:105; Mendez 1956:168–170; Hopkins and Rothschild 1962: 389; Jellison and Senger 1973:46; Lewis 1974:155; Jellison and Senger 1976:79.

*Megarthroglossus divisus divisus*: Jellison and Good 1942:83; Ewing and Fox 1943:112; Hubbard 1947: 300–301; Holland 1949a:9; Holland 1949b:99; Tipton 1950:64; Hopkins 1952:363–365; Allred 1952:67–75; Beck et al. 1953:43–52; Jellison, Locker, and Bacon 1953:104; Morlan 1954:446–448; Beck 1955:1–64; Morlan 1955:93–125; Wiseman 1955:1–28; Mendez 1956: 168–170; Stark 1959:101; Hopkins and Rothschild 1962:



Figs. 39–42. Males, sterna VIII and IX; 39, *Megarthroglossus cavernicolus*; 40, *M. becki*; 41–42. claspers; 41, *M. cavernicolus*; 42, *M. becki*.

387; Jellison and Glesne 1967:168–170; Tipton and Saunders 1971:18; Jellison and Senger 1973:44–45; Pratt and Stark 1973:1–42; Lewis 1974:155.

Type host.— *Tamiasciurus hudsonicus fremonti.*

Type locality.— Georgetown, Clear Creek Co., Colorado.

Type specimens.— United States National Museum, Washington, D.C.

Diagnosis.— Male: The posterior margin of sternum VIII is sinuate, with an evenly convex ventrolateral lobe. The dorsal margin of the aedeagus is straight or if a hump is present it is less than 10 microns in height. The inner fovea of the immovable process is less than 20 microns in length. The spur of the crochet is less than 60 microns in length. Segment V of the labial palp exceeds 170 microns in length. *Megarthroglossus divisus* most closely resembles *M. cavernicolus* and *M. wilsoni,* but the characters given above are diagnostic.

Female: The bulga is compressed. The sternum VII sinus ratio is less than 3.00. Segment V of the labial palp is more than 270 microns in length (average length). *Megarthroglossus divisus* most closely resembles *M. smiti,* but the two species may be separated in that the hilla ratio is less than 1.20 and the bulga ratio is less than 1.70 (see Fig. 34) in *M. divisus.*

Distribution.— Arizona: Apache County. California: San Bernardino and Mono counties. Colorado: Clear Creek and Montezuma counties. Idaho: National Reactor Testing Site including parts of Bingham, Butte, and Jefferson counties. Montana: Beaverhead, Flathead, Lake, Madison, Missoula, Park, Powell, and Ravalli counties. New Mexico: Bernalillo, Colfax, Lincoln, McKinley, Oterno, Rio Arriba, Sandoval and Santa Fe counties. Nebraska: Scotts Bluff County. Oregon: Wallowa County. Texas: Donley County. Utah: Cache, Carbon, Duchesne, Iron, Kane, San Juan, Sevier, Tooele, Uintah, Utah, Wasatch, and Wayne counties. Wyoming: Albany and Waskokie counties. Canada: Alberta, British Columbia.

Material examined.— California: (San Bernardino Co.) 2 ♂, ex rodent nest, Big Bear Lake, 30-X-1958, Poll and Perry (Barnes). Colorado: (Montezuma Co.) 1 ♂, 1 ♀, ex *Peromyscus truei/P. maniculatus,* Mesa Verde National Park, 11-I-1962, Douglas (BYU); 3 ♀, same host, same location, 21-XI-1961, Douglas (BYU); 1 ♀, same host, same location, 25-X-1961, Douglas (BYU); 2 ♀, same host, same location, 13-X-1961, Douglas (BYU); 1 ♂, 1 ♀, same host, same location, 18-X-1961, Douglas (BYU); 1 ♀, same host, same location, 14-X-1961, Douglas (BYU); 1 ♂, same host, same location, 27-X-1961, Douglas (BYU); 1 ♂, 1 ♀, same host, same location, 24-XI-1961, Douglas (BYU). Idaho: (National Reactor Testing Site), 1 ♂, ex *Peromyscus maniculatus,* Idaho Falls, 16-I-1967, BYU; 1 ♀, ex *Neotoma cinerea,* same location, 22-VIII-1967, BYU; 3 ♂, 5 ♀, ex *Neotoma cinerea* nest, same location, 17-II-1967. Montana: (Flathead Co.) 7 ♂, 4 ♀, ex *Neotoma* nest, no specific location, 4-III-1963, Senger; 6 ♂, 10 ♀, same host, same location, III-1963, Senger; (Lake Co.) 2 ♂, 3 ♀, ex *Neotoma* nest, Ravalli, 15-IV-1963, Senger; (Missoula Co.) 1 ♀, ex *Neotoma cinerea,* Rattlesnake Creek, 9-XI-1957, Senger; 6 ♂, 12 ♀, ex *Neotoma* nest, no specific location, III-1963, Senger; (Park Co.) 1 ♂, ex *Peromyscus maniculatus,* Frozen Lake, no date given, Pattie (Senger); (Ravalli Co.) 8 ♂, 7 ♀, ex *Neotoma* nest, no specific location, no date given, Senger; 7 ♂, 15 ♀, same host, 8 Mile Creek, 1962, Senger; 1 ♀, ex mouse nest, Airport, 3-I-1963, Senger; 13 ♂, 38 ♀, ex *Neotoma* nest, 8 Mile Creek, 29-XII-1962, Senger; 1 ♀, ex pine squirrel nest, no specific location, 17-II-1963, Senger. New Mexico: (McKinley Co.) 1 ♂, ex *Peromyscus maniculatus,* no specific location, 12-V-1967, CDC; (Rio Arriba Co.) 1 ♂, ex *Peromyscus boylii,* Lindrith, 12-1-1951, CDC. Nebraska: (Scotts Bluff Co.) 1 ♂, ex *Peromyscus* nest, Morrill, 24-V-1949, CDC. Utah: (Carbon Co.) 1 ♀, ex *Tamiasciurus hudsonicus,* Schofield, 12-VIII-1960, Pritchett (BYU); (Duchesne Co.) 1 ♀, same host, Duchesne, 7-VIII-1953, Killpack and Coffey (BYU); (Iron Co.) 1 ♀, ex *Tamiasciurus fremonti,* Cedar Breaks, Brianhead, 7-VIII-1949, Tipton (BYU); 1 ♀, ex *Tamiasciurus hudsonicus,* same location, 23-VI-1960, Pritchett (BYU); (Kane Co.) 2 ♂, 1 ♀, ex *Peromyscus truei,* 2-XII-1971, BYU; 1 ♂, same host, 13-XI-1971, BYU; (Sevier Co.) 3 ♂, ex *Tamiasciurus hudsonicus,* Koosharem, 22-VII-1953, Beck et al. (BYU); (Uintah Co.) 4 ♀, ex *Peromyscus maniculatus* nest, Jensen, 7-XI-1952, Beck and Beck (BYU); 1 ♀, ex *Peromyscus maniculatus*, 8-XI-1952, Beck and Beck (BYU); (Wayne Co.) 23 ♂, 17 ♀, ex *Tamiasciurus fremonti* nest, Elkhorn RS., 9-VIII-1952, Killpack et al. (BYU). WYOMING: (Albany Co.) 1 ♂, 1 ♀, ex *Neotoma*, no specific location. 9-VII-1943 (CDC); (Waskaki Co.) 2 ♂, 1 ♀, ex *Sylvilagus audubonii*, no specific location, 1-XI-1979, Carter (CDC).

HOST SYNONYMY.— *Tamiasciurus fremonti* = *Tamiasciurus hudsonicus fremonti.*

DISCUSSION.— *Megarthroglossus divisus* has been collected in all western states except Washington and Nevada. It probably occurs in these states as well, because the hosts on which it occurs most frequently (i.e. *Tamiasciurus, Peromyscus*, and *Neotoma*) occur there. It has also been collected from Alberta and British Columbia, Canada. Mendez (1956) and Hopkins and Rothschild (1962) treated this taxon as two subspecies: *M. divisus divisus* and *M. divisus exsecatus.* Upon close examination, there appeared to be three populations: *M. d. divisus* associated with *Tamiasciurus*; *M. d. exsecatus* associated with *Neotoma*; and a third population associated with *Peromyscus.* Measurements of various morphological characters showed the third population to be intermediate between the other two. However, the three populations are extremely difficult to separate since they have overlapping distributions. It appears that the three populations represent a single species and there are no characters which can be used consistently for subspecies discrimination. More than 300 specimens have been examined, and more than 100 specimens have been measured.

### *Megarthroglossus jamesoni* Smit

Figs. 54, 66, 67, 84, 100

*Megarthroglossus jamesoni* Smit 1953:202–203; Mendez 1956:170; Hopkins and Rothschild 1962:376; Lewis 1974:155.

TYPE HOST.— *Neotoma cinerea* nest.

TYPE LOCALITY.— Pine Nut Mts., Douglas Co., Nevada.

TYPE SPECIMENS.— British Museum (Natural History), South Kensington, London, England.

DIAGNOSIS.— MALE: The median dorsal lobe of the aedeagus is reduced to a short blunt lobe in *M. jamesoni* and *M. sierrae* and this character may be used to separate these species from *M. smiti. Megarthroglossus sierrae* and *M. jamesoni* may be distinguished from each other in that the latter has a hump on the dorsal margin of the aedeagus that exceeds 30 microns; segment V of the labial palp is more than 220 microns in length; the inner fovea of the immovable process is more than 30 microns below the dorsal margin of the clasper and it is submarginal; and the ventrolateral lobe of sternum VIII is truncate.

FEMALE: The bulga is not compressed; the width of the hilla exceeds 40 microns which is broader than either *M. sicamus* or *M. cavernicolus.* The spermathecae of *M. jamesoni* and *M. cavernicolus* are similar in that both lack the posteriorly directed hilla observed in *M. sicamus.* Segment V of the labial palp exceeds 270 microns in length, but it is less than 230 microns in *M. cavernicolus.*

DISTRIBUTION.— CALIFORNIA: Lassen County. NEVADA: Douglas County.

MATERIAL EXAMINED.— CALIFORNIA: (Lassen Co.) 1 ♂, 1 ♀, ex *Neotoma cinerea*, Fort Sage Mts., 26-II-1975, Smith and Nelson; 1 ♂, 1 ♀, ex *Neotoma lepida*, same location, same date, Smith and Nelson. NEVADA: (Douglas Co.) 2 ♂, 3 ♀, ex *Neotoma cinerea* nest, Pine Nut Mts., 25-III-1951, Jameson.

DISCUSSION.— *Megarthroglossus jamesoni* has been collected only from species of *Neotoma* and their nests. Further collections will be necessary to make any meaningful statement regarding host associations of this flea. Mendez (1956) examined 2 males and 1 female from Malheur Co., Oregon, but declined to refer them to *M. jamesoni* because of the limited amount of study material. He observed slight differences in the male genitalia of this flea, but did not include drawings or host data. Subsequently, specimens of *M. jamesoni* were collected in northern California. It would have been helpful to compare the Oregon specimens with those from California and Nevada.

### *Megarthroglossus procus muiri* Augustson

Figs. 49, 61, 78, 90, 101

*Megarthroglossus muiri* Augustson 1953:122–125; Mendez 1956:163, 171; Jellison and Glesne 1967:172.

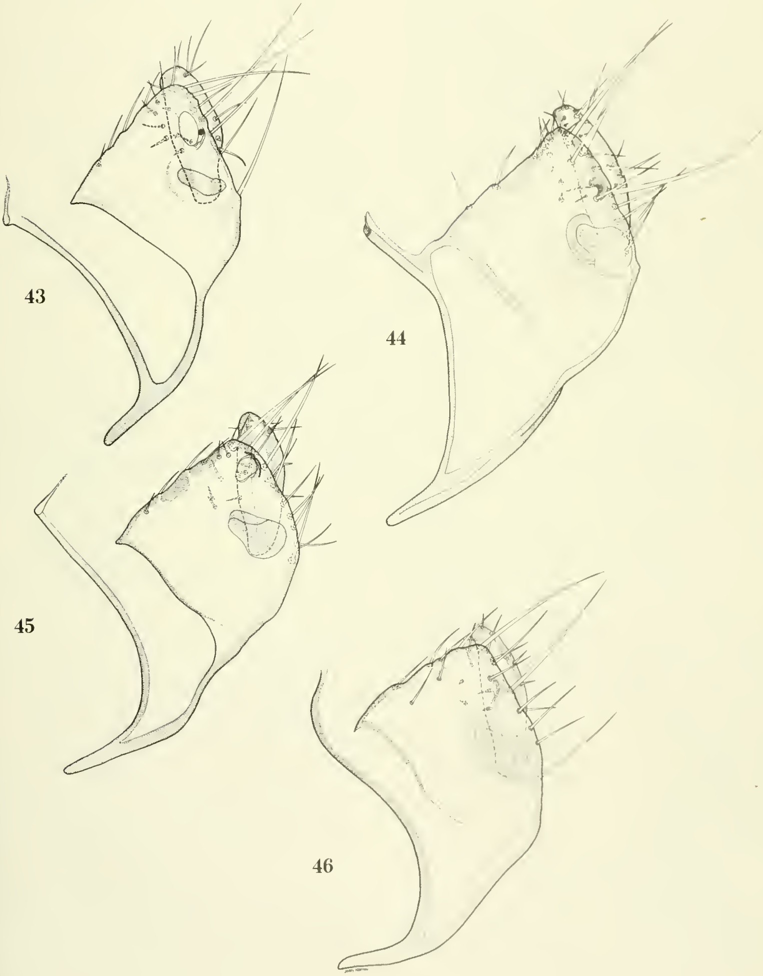
*Megarthroglossus procus muiri*: Hopkins and Rothschild 1962:374.

TYPE HOST.— *Tamiasciurus douglasi albolimbatus* and *Sorex palustris navigator*.

TYPE LOCALITY.— Tully's Hole, Fresno Co., California.

TYPE SPECIMENS.— Allan Hancock Foundation, University of Southern California, Los Angeles, California.

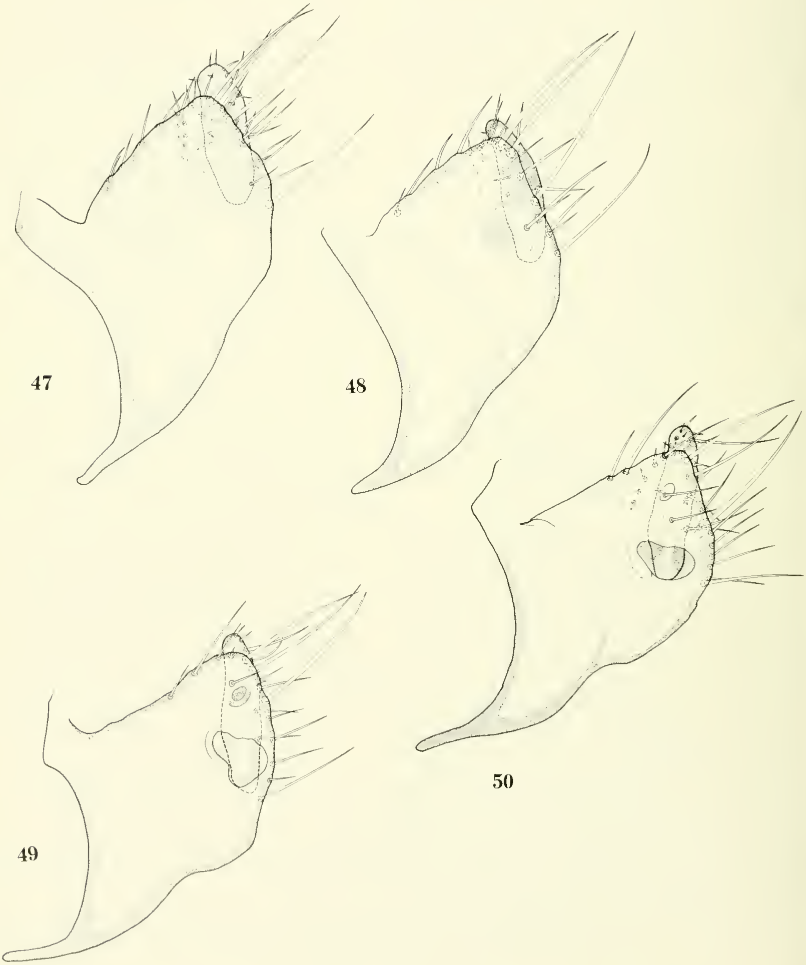
DIAGNOSIS.— MALE: The two subspecies of *Megarthroglossus procus* may be separated from all other species of *Megarthroglossus* by the following characters: The ventrolateral



Figs. 43–46. Males, claspers; 43, *Megarthroglossus wilsoni*; 44, *M. sicamus*; 45, *M. bisetis*; 46, *M. weaveri*.

lobe of sternum VIII is divided into an upper evenly convex lobe and a lower acuminate lobe separated by a sharp sinus; the crochet does not possess the well-defined spur observed in other species such as *M. divisus*; however, a short lobe less than 10 microns may be present in some. *Megarthroglossus p. muiri* can be distinguished from *M. p. procus* in that the latter has a median dorsal lobe which is less than 20 microns in width; segment V of the labial palp is 130 microns in length and the sinus in sternum VIII exceeds 45 microns in depth.

Female: Usually there is no sinus in the



Figs. 47–50. Males, claspers; 47, *Megarthroglossus divisus* (Wayne Co., Utah); 48, *M. divisus* (Ravalli Co., Montana); 49, *M. procus muiri*; 50, *M. p. procus*.

posterior margin of sternum VII, but, if present, it is less than 10 microns in depth; there are 3 antepygidial bristles per side; the pronotal comb has 6 spines per side; the hilla ratio exceeds 1.50, and the bulga ratio exceeds 1.50 (Fig. 34). These characters are adequate for separation of *M. p. procus* and *M. p. muiri*, but the presence of males in a collection aids greatly in subspecific discrimination.

Distribution.— California: Fresno, Mono, and Plumas counties.

Material examined.— California: (Fresno Co.) 1 ♂, holotype, ex *Tamiasciurus douglasi albolimbatus*, Tully's Hole, 25-VIII-1941, Auguston; 1 ♀, allotype, ex *Sorex* sp. *navigator*, Tully's Hole, 24-VIII-1941, Augustson; (Plumas Co.) 1 ♂, ex *Peromyscus maniculatus* 6.4 km E of Quincy, 1520 m, 24-X-1949, Jameson.

Host synonymy.— *Tamiasciurus douglasi albolimbatus* = *Tamiasciurus hudsonicus albolimbatus.*

Discussion.— *Megarthroglossus procus muiri* has been collected from species of *Tamiasciurus*, *Ochotona*, and *Sorex*. Additional specimens are necessary to determine host associations of this flea. It has been collected only in California; however, it is likely that it occurs in Nevada, Oregon, and Washington as well.

## *Megarthroglossus procus procus* Jordan & Rothschild

Figs. 50, 62, 76, 77, 88, 89, 101

*Megarthroglossus procus* Jordan and Rothschild 1915:47–50; Wagner 1930:130; Spencer 1936:14; Mail and Holland 1940:126; Hubbard 1940:37(4); Augustson 1941:151; Ewing and Fox 1943:113; Hubbard 1943:1–12; Hatt 1943:311–345; Hubbard 1947:297; Hubbard 1949:126; Holland 1949a:10; Holland 1949b:100; Tipton 1950:63; Hopkins 1952:363–365; Mendez 1956:164–166; Jameson and Brennan 1957:45–54; Stark 1959:100; Beck 1966:76; Beck and Allred 1966:13; Jellison and Glesne 1967:172; Tipton and Saunders 1971:18; Mendez and Haas 1972:285–288; Mendez and Haas 1973:1132; Lewis 1974:155; Egoscue 1976:478; Jellison and Senger 1976:80.

*Megarthroglossus similis* Wagner 1936:196; Mail and Holland 1939:126; Jellison and Good 1942:84; Ewing and Fox 1943:113; Hubbard 1943:1–12; Hubbard 1947:302; Holland 1949a:10; Holland 1949b:99; Jellison, Locker, and Bacon 1953;107; Mendez 1956:175.

*Megarthroglossus senisles* (sic) Spencer 1936:14.

*Megarthroglossus procus oregonesis* Hubbard 1947:299–300; Jellison, Locker, and Bacon 1953:105.

*Megarthroglossus procus procus* Hubbard 1947:297, Jellison, Locker, and Bacon 1953.105; Hopkins and Rothschild 1962:371–372.

Type host.— *Spilogale* sp.

Type locality.— Chilliwack, British Columbia, Canada.

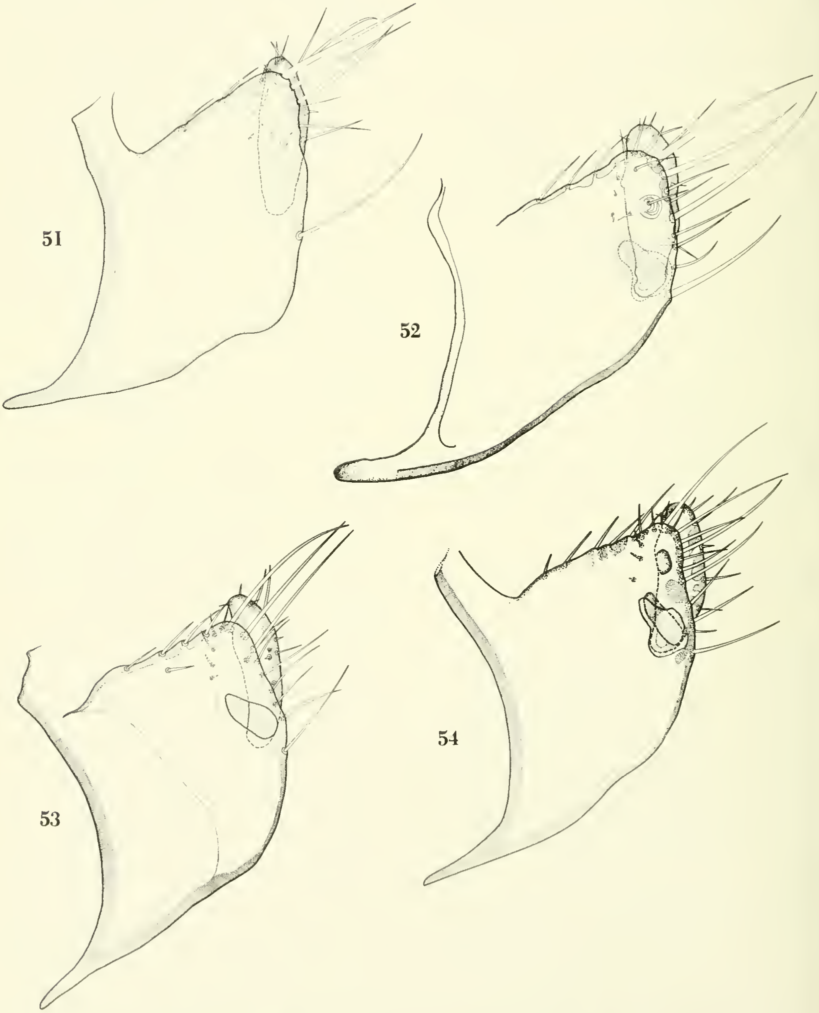
Type specimens.—British Museum (Natural History), London.

Diagnosis.— Male: The two subspecies of *M. procus* have a divided ventrolateral lobe of sternum VIII which is not present in other species of the genus *Megarthroglossus*. *M. p. procus* may be separated from *M. p. muiri* in that in the former the median dorsal lobe of the aedeagus is more than 20 microns in width; segment V of the labial palp is more than 140 microns in length; and the sinus in sternum VIII is less than 45 microns in depth.

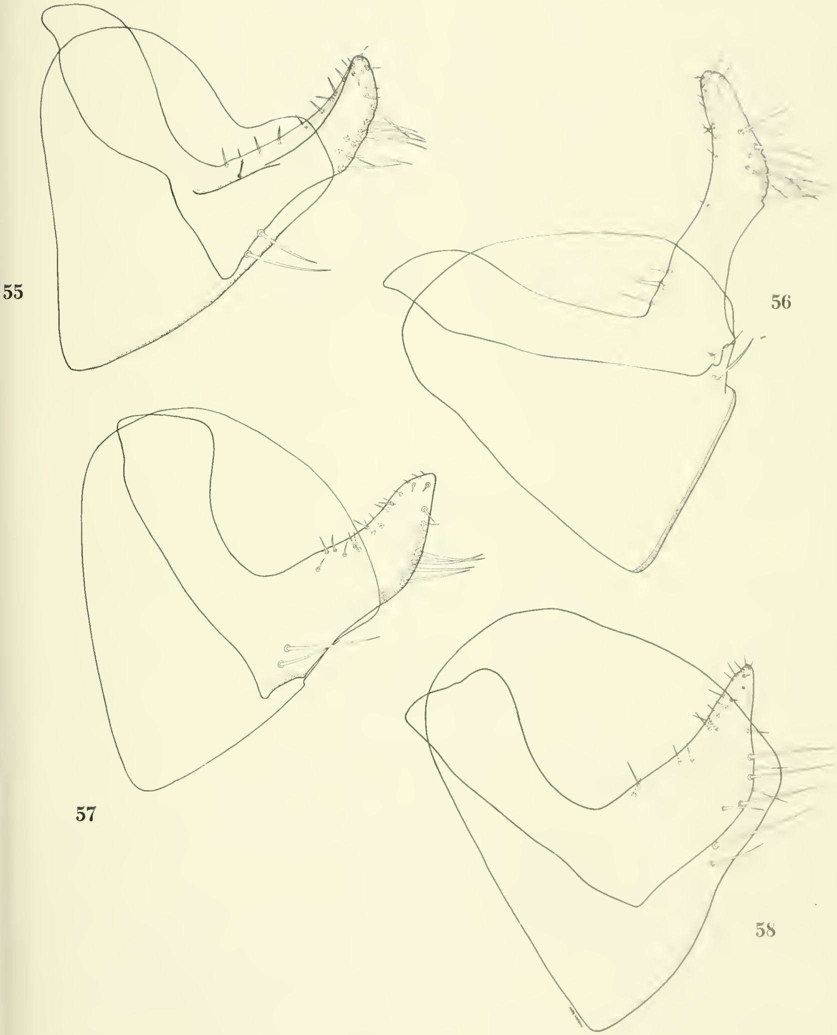
Female: The pronotal comb has 6–8 spines per side; there are 2 or 3 antepygidial bristles; there is no sinus in the caudal margin of sternum VII or, if it is present, it is less than 10 microns in depth; the hilla ratio is less than 1.20 and the bulga ratio is less than 1.40. However, a definite identification is possible only if male specimens are available.

Distribution.— California: Eldorado, Plumas, and San Bernardino counties. Colorado: Montezuma County. Nebraska: Sioux County. Nevada: Douglas and Washoe counties. Oregon: Hood River, Linn, and Washington counties. Washington: Skagit, Whatcom, and Yakima counties. Wyoming: Laramie and Weston counties. Utah: Utah County. Canada: British Columbia.

Material examined.— California: (El Dorado Co.) 2 males, 1 female, ex chipmunk, no specific location, X-1936, Eskey (Jellison); (San Bernardino Co.) 1 male, ex *Citellus lateralis*, Big Bear Lake, 13-V-1955, Martin. Nevada: (Washoe Co.) 1 ♂, 1 ♀, ex chipmunk, no specific location, X-1936, Eskey (Jellison). Oregon: (Linn Co.) 1 ♀, ex *Tamiasciurus douglasi*, 2.4 km N of Big Lake, 1-XI-1969, Maser; 1 ♂, ex *Eutamias townsendi*, T14S, R6E, NE ¼, Sec. 28, 1400 m, 12-IX-1972, Maser; 1 ♀, ex *Peromyscus maniculatus*, same location, same elevation, same date, Maser; 1 ♀, ex *Glaucomys sabrinus*, T15S, R15E, SE¼, Sec. 11, 26-IX-1972, Maser; 1 ♀, same host, T25S, R6E, SE¼, Sec. 11, 1040 m, same date, Maser; 1 ♀, same host, T15S, R5E, SG¼, Sec. 11, same elevation, 28-IX-1972, Maser; (Washington Co.) 1 ♂, 1 ♀, paratypes, ex *Tamiasciurus d. douglasi*, Caston, 7-III-1932, Hubbard (BYU); 1 ♂, 1 ♀, paratypes same host, same location, 8-III-1932, Hubbard (BYU). WASHINGTON: (Skagit Co.) 2 ♂, 7 ♀, ex *Neotoma* nest, Blanchard Caves, 19-III-1966, Senger; 3 ♀, same host, same location, XII-1965, Senger; 10 ♂, 12 ♀, same host, same location, 20-XI-1966, Senger; 15 ♂, 20 ♀, same host, same location, 5-XI-1967, Senger; 1 ♀, same host, same location, 18-IX-1967, Senger; 3 ♂, 5 ♀, same host, same location, 17-XI-1968, Senger; 3 ♂, 2 ♀, same host, same location, 9-III-1968, Senger; 6 ♂, 17 ♀, same host, same location, XI-1965, Senger; 15 ♂, 5 ♀,



Figs. 51–54. Males, claspers; 51, *Megarthroglossus smiti*; 52, *M. spenceri*; 53, *M. sierrae*; 54, *M. jamesoni*.



Figs. 55–58. Males, sterna VIII and IX; 55, *Megarthroglossus wilsoni*; 56, *M. sicamus*; 57, *M. bisetis*, 58, *M weaveri*.

same host, same location, 20-XI-1965, Senger; 1 ♀, same host, same location, III-1965, Senger; 24 ♂, 21 ♀, same host, Lizzard Caves, 19-II-1966, Senger; 2 ♂, 6 ♀, same host, same location, 15-I-1966, Senger; 2 ♂, 1 ♀, same host, same location, XI-1965, Senger; (Wheaton Co.) 5 ♂, 5 ♀, same host, Glacier, X-1963, Senger; 1 ♀, ex nest in old fin snag, Chuckanut Mt., 14-II-1965, Senger; 1 ♀, ex nest in fallen snag, Silver-Fir Campground, Nooksack River, 3-IX-1966, Senger; (Yakima Co.) 2 ♀, ex *Ochotona princeps*, Chinook Pass, 16-IX-1966, Senger; CANADA: (British Columbia) 1 ♂, 1 ♀, ex *Tamiasciurus douglasi*, 11.2 km S of Boston Bar, 14-III-1948, Holland; 1 ♂, ex *Glaucomys* sp., Grouse Mt., Vancouver, 21-I-1947, Dowding (Holland); 1 ♂, ex *Sciurus douglasi*, Gambien Island, 21-II-1943, Holland; 1 ♀, ex squirrel, Cultus Lake, 31-X-1947, Leavens (Holland); 1 ♀, ex *Tamiasciurus* sp., Huntingdon, 16-XI-1946, Racey (Holland); 1 ♀, ex *Rattus norvegicus*, Vancouver, 7-I-1945, Holland.

HOST SYNONYMY.— *Tamiasciurus d. douglasi* = *Tamiasciurus hudsonicus douglasi*; *Sciurus douglasi* = *Tamiasciurus hudsonicus douglasi*; *Citellus lateralis* = *Spermophilus lateralis.*

DISCUSSION.— Most of the specimens in Dr. C. M. Senger's collection were taken from species of *Neotoma* in Washington. However, it has been collected from several other hosts, principally, *Tamiasciurus hudsonicus douglasi.*

### *Megarthroglossus sicamus* Jordan & Rothschild

Figs. 44, 56, 81, 91, 101

*Megarthroglossus sicamus* Jordan and Rothschild 1915:50–52; Dalla Torre 1924:17; Wagner 1936:196; Mail and Holland 1939:126; Jellison and Good 1942:84; Ewing and Fox 1943:113; Hubbard 1943:1–12; Costa Lima and Hathaway 1946:125; Hubbard 1947:302; Holland 1949a:10; Holland 1949b:101; Jellison, Locker and Bacon 1953:104; Mendez 1956:173–174; Hopkins and Rothschild 1962:382; Lewis 1974:155.

TYPE HOST.— *Canis latrans.*

TYPE LOCALITY.— Eagle River, Sicamous, British Columbia, Canada.

TYPE SPECIMENS.— British Museum (Natural History), South Kensington, London, England.

DIAGNOSIS.— MALE: The caudal margin of sternum VIII is evenly convex in *M. sicamus*, *M. bisetis* and *M. weaveri*. However, *M. sicamus* has a hump on the dorsal margin of the aedeagus that is more than 30 microns while it is less than 10 microns in the other two species. Other species which have a hump on the dorsal margin of the aedeagus include *M. spenceri*, *M. smiti*, *M. sierrae*, *M. jamesoni*, and *M. becki*. The inner fovea of the immovable process of the clasper is more than 60 microns below the dorsal margin in *M. sicamus* but not in the other five species mentioned.

FEMALE: No specimens were available for study. On the basis of the literature, it appears that *M. sicamus* most closely resembles *M. cavernicolus* and *M. jamesoni*. The hilla appears to be less than 40 microns in width but more than 40 microns in *M. jamesoni*. In *M. sicamus* the hilla is bent toward the bulga but in *M. cavernicolus* it is not.

DISTRIBUTION.— CANADA: British Columbia.

MATERIAL EXAMINED.— CANADA: (British Columbia) 1 ♀, ex *Lynx* sp., Kamloops, 20-V-1946, Carter (Holland); 1 ♀, ex *Neotoma*, Pavilion Lake, Pavilion, 5-VII-1950, Holland; 1 ♂, ex *Canis latrans*, Eagle River, Sicamous, 6-IX-1903, Dippie (Smit).

DISCUSSION.— *Megarthroglossus sicamus* has been collected only from British Columbia. Because of the paucity of specimens, reliable host association data are lacking.

### *Megarthroglossus sierrae* Auguston

Figs. 53, 65, 69, 92, 100

*Megarthroglossus divisus sierrae* Augustson 1953: 125–126; Jellison and Glesne 1967:170; Jellison and Senger 1976:79.

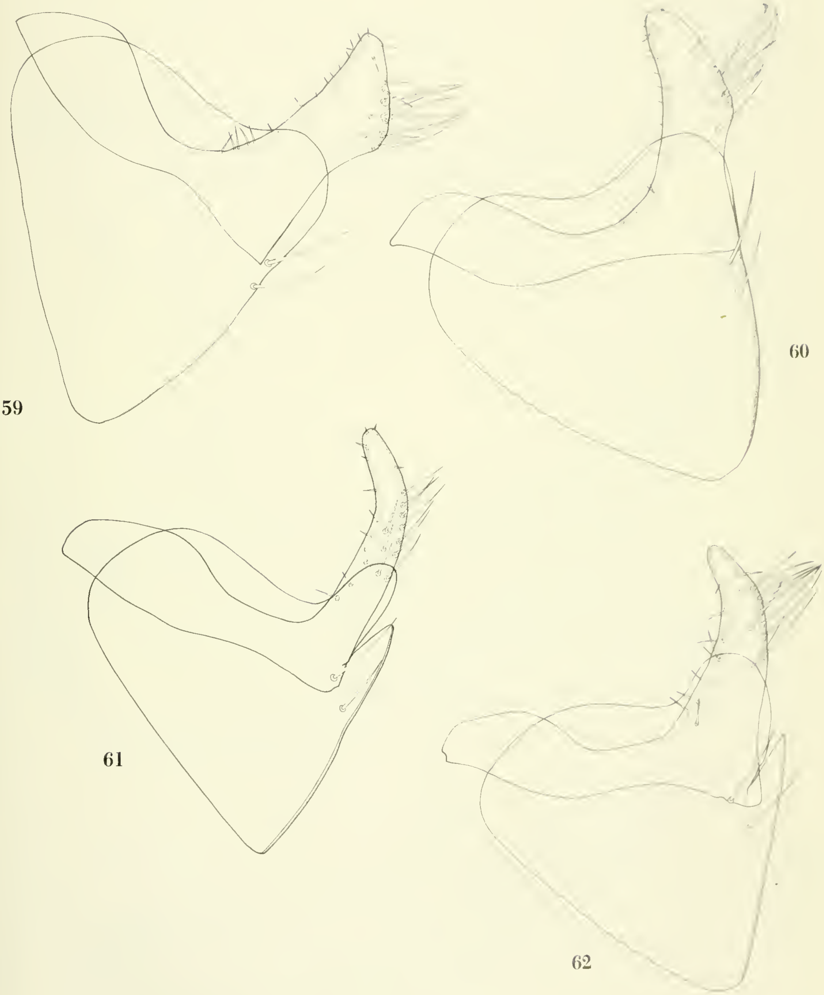
*Megarthroglossus sierrae* Mendez 1956:174; Hopkins and Rothschild 1962:378; Lewis 1974:155; Jellison and Senger 1976:80.

TYPE HOST.— *Ochotona schisticeps muiri* and *Tamiasciurus douglasi albolimbatus.*

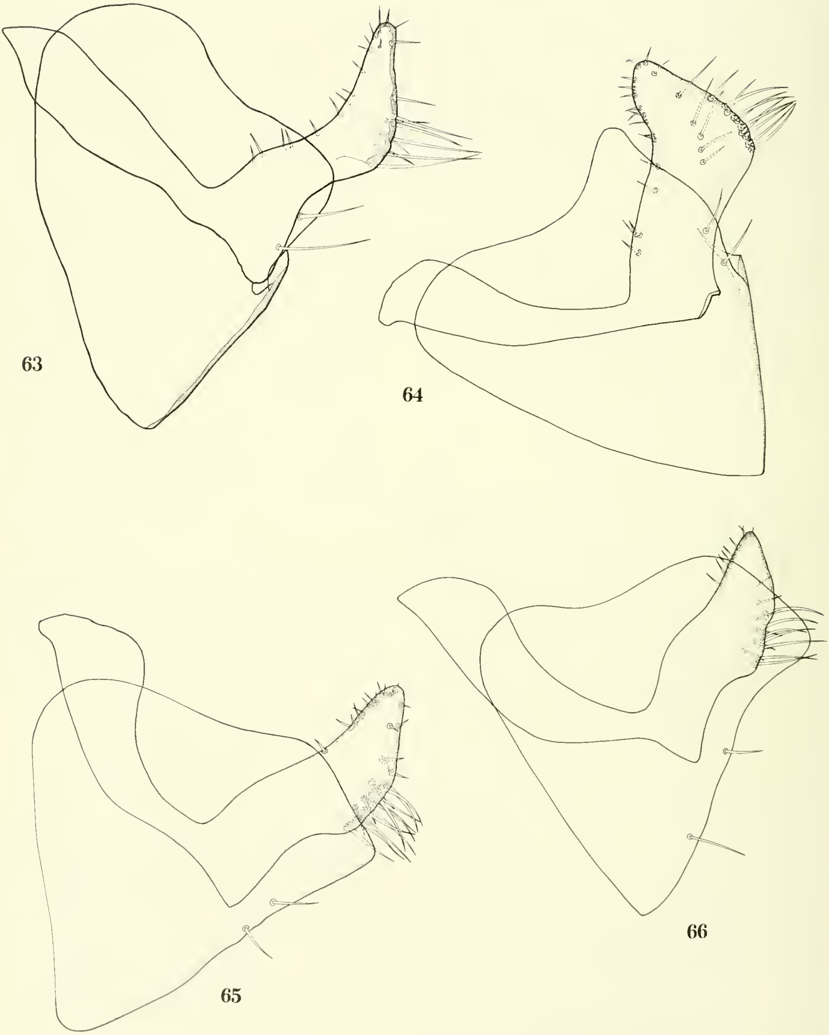
TYPE LOCALITY.— Cascade Valley, Fresno Co., California.

TYPE SPECIMENS.— Allan Hancock Foundation, University of Southern California, Los Angeles, California.

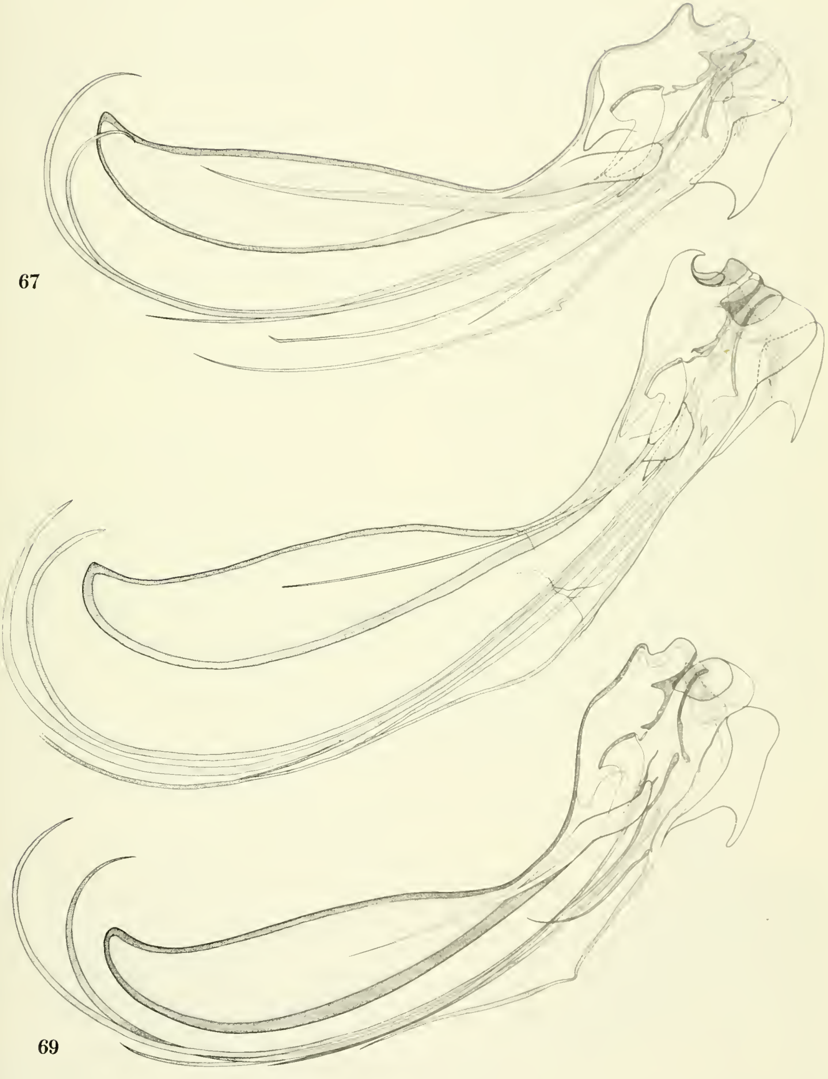
DIAGNOSIS.— MALE: *M. sierrae* and *M. jamesoni* resemble each other in that the me-



Figs. 59–62. Males, sterna VIII and IX; 59 *Megarthroglossus divisus* (Wayne Co., Utah); 60, *M. divisus* (Ravalli Co., Montana); 61, *M. procus muiri*; 62, *M. p. procus*.



Figs. 63–66. Males, sterna VIII and IX; 63, *Megarthroglossus spenceri*; 64, *M. smiti*; 65, *M. sierrae*; 66, *M. jamesoni*.



Figs. 67–69. Males, aedeagus; 67, *Megarthroglossus jamesoni*; 68, *M. becki*; 69, *M. sierrae*.

dian dorsal lobe of the aedeagus is reduced to a short blunt lobe in both species. *M. sierrae* may be distinguished from *M. jamesoni* on the basis of the following characters: The hump on the dorsal margin of the aedeagus is less than 20 microns; segment V of the labial palp is less than 220 microns in length; the inner fovea of the immovable process is marginal, and the ventrolateral lobe of sternum VIII is subtruncate.

FEMALE: *M. sierrae* and *M. procus* ssp. each lack a sinus in the caudal margin of sternum VII, but, if a sinus is present, it is less than 10 microns in depth. In *M. sierrae* the vertical portion of the hilla is more than 115 microns and the hilla is more than 50 microns in width; metatarsal segment I is more than 300 microns in length.

DISTRIBUTION.— CALIFORNIA: Fresno and Mono counties.

MATERIAL EXAMINED.— CALIFORNIA: (Fresno Co.) 1 ♂, holotype, ex *Ochotona schisticeps muiri*, Cascade Valley, 27-VIII-1941, Augustson; (Mono Co.) 1 ♀, allotype, ex *Tamiasciurus douglasi albolimbatus*, Mammoth Lakes, 31-VII-1939, Augustson.

HOST SYNONYMY.— *Tamiasciurus douglasi albolimbatus* = *Tamiasciurus hudsonicus albolimbatus*.

DISCUSSION.— *Megarthroglossus sierrae* has been reported only from the type locality in California on *Tamiasciurus* and *Ochotona*. *Megarthroglossus sierrae, M. divisus*, and *M. procus* overlap in California in both ecological and geographical distribution. Additional data is needed to clarify the relationships of these species.

### *Megarthroglossus smiti* Mendez

Figs. 51, 64, 79, 93, 101

*Megarthroglossus smiti* Mendez 1956:175; Howell 1955:35–48; Howell 1957:566–573; Parker and Howell 1959:597–604; Stark 1959:99; Hopkins and Rothschild 1962:385; Jellison and Glesne 1967:173; Tipton and Saunders 1971:18; Mendez and Haas 1973:1132; Jenkins and Grundmann 1973:81; Lewis 1974:155; Egoscue 1976:479; Jellison and Senger 1976:80.

TYPE HOST.— *Neotoma lepida* nest.

TYPE LOCALITY.— Lynndyl, Millard Co., Utah.

TYPE SPECIMENS.— United States National Museum, Washington, D.C.

DIAGNOSIS.— MALE: *M. smiti*, like *M. sierrae* and *M. jamesoni*, has a hump on the dorsal margin of the aedeagus; however, it is more pronounced in *M. smiti* than in *M. sierrae* and less so than in *M. jamesoni*. There is a considerable amount of variability in this character and so its taxonomic value is questionable. In *M. smiti* the median dorsal lobe is produced into a long process which curves caudally at the apex, and sternum VIII has an undulating posterior margin with a short, subacuminate lobe.

FEMALE: *M. smiti, M. divisus, M. becki*, and *M. wilsoni* are similar in many respects. *M. smiti* may be distinguished from the latter two species in that the depth to width ratio of the sinus in sternum VII is more than 3.0; segment V of the labial palp is more than 270 microns in length (average). *Megarthroglossus smiti* may be separated from *M. divisus* in that the sternum VII sinus ratio is more than 4.0; the hilla ratio exceeds 1.20 and the bulga ratio exceeds 1.80.

DISTRIBUTION.— NEVADA: Nye County. UTAH: Beaver, Emery, Juab, Millard, Tooele, and Utah counties.

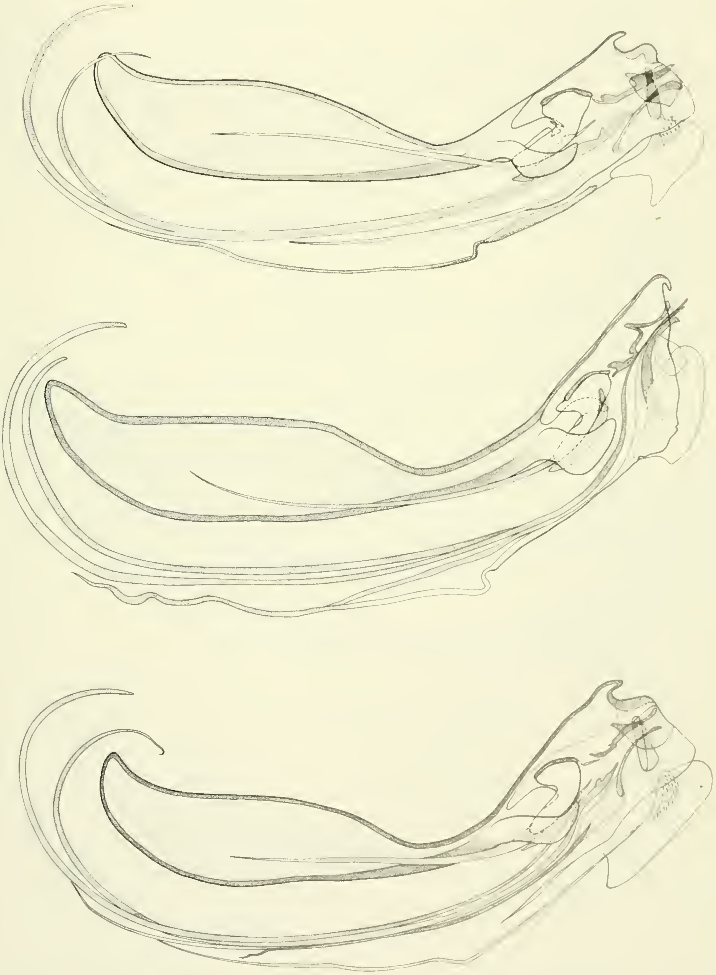
MATERIAL EXAMINED.— NEVADA: (Nye Co.) 1 ♂, ex *Neotoma lepida*, Mercury, 6-XI-1961, AEC-NRTS (BYU). UTAH: (Juab Co.) 5 ♂, 2 ♀, ex *Neotoma lepida* nest, Jericho, 29-IV-1954, J. F. Howell; 1 ♂, 1 ♀, ex *N. lepida* 4.5 km N Jericho, 8-V-1954, J. F. Howell; 9 ♂, 16 ♀, ex *N. lepida* nest, Jericho, 8-X-1954, J. F. Howell, 5 ♂, 19 ♀, ex same host, same location, 29-X-1954, J. F. Howell; 3 ♂, 2 ♀, ex *N. lepida*, same location, same date, J. F. Howell; 2 ♂, 2 ♀, ex *N. lepida* nest, same location, 12-XI-1954, J. F. Howell; 15 ♂, 30 ♀, ex same host, same location, 2-XII-1954, J. F. Howell; 4 ♂, 4 ♀, ex same host, same location, 7-I-1955, J. F. Howell; (Millard Co.) 4 ♂, 5 ♀ paratypes, ex *N. lepida*, Lynndyl, 17-XI-1951, Barnum and Moore; (Utah Co.) 1 ♂ paratype, ex *N. lepida*, Chimney Rock Pass, 15-X-1949, D. M. Allred; 7 ♂, 6 ♀ paratypes, ex same host, Rush Valley, 9-XI-1951, Barnum and Moore; 3 ♂, ex *Neotoma* nest, Chimney Rock Pass, 25-X-1968, Clark and Mathis.

DISCUSSION.— *Megarthroglossus smiti* has been collected in Utah and Nevada. The known geographical distribution of the host, *Neotoma lepida*, is greater than the known geographical distribution of *M. smiti*. More extensive collecting of the host in Arizona, California, Idaho, and Oregon will likely expand the known distribution of *M. smiti.*

### *Megarthroglossus spenceri* Wagner
Figs. 52, 63, 80, 94, 101)

*Megarthroglossus spenceri* Wagner 1936:196; Spencer 1935:14; Mail and Holland 1939:126; Jellison and Good 1942:84; Ewing and Fox 1943:114, Hubbard 1943:1–12, Costa Lima and Hathaway 1946:126; Hubbard 1947 303–304; Holland 1949a:10; Holland 1949b:101; Jellison, Locker, and Bacon 1953:107; Mendez 1956:177; Hopkins and Rothschild 1962:383–384, Lewis 1974:155.

*Megarthroglossus pygmaeus* Wagner 1936:196; Jellison and Good 1942:84; Ewing and Fox 1943:113, Hubbard 1943:1–12; Costa Lima and Hathaway 1946:126; Hubbard 1947:303; Holland 1949a:10; Holland 1949b·



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Figs. 70–72. Males, aedeagus; 70, *Megarthroglossus cavernicolus*; 71, *M. weaveri*, 72, *M. bisetis*.

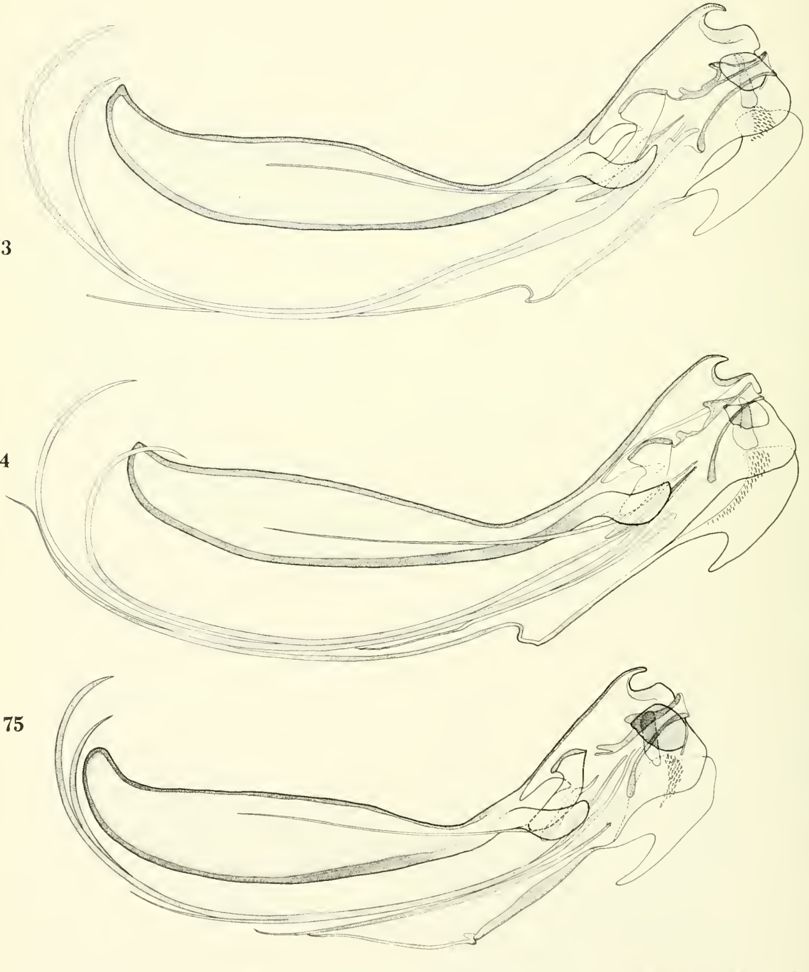
100–101; Jellison, Locker, and Bacon 1953:106; Mendez 1956:172–173; Hopkins and Rothschild 1962:384.

TYPE HOST.— *Neotoma cinerea* and *Ochotona princeps*.

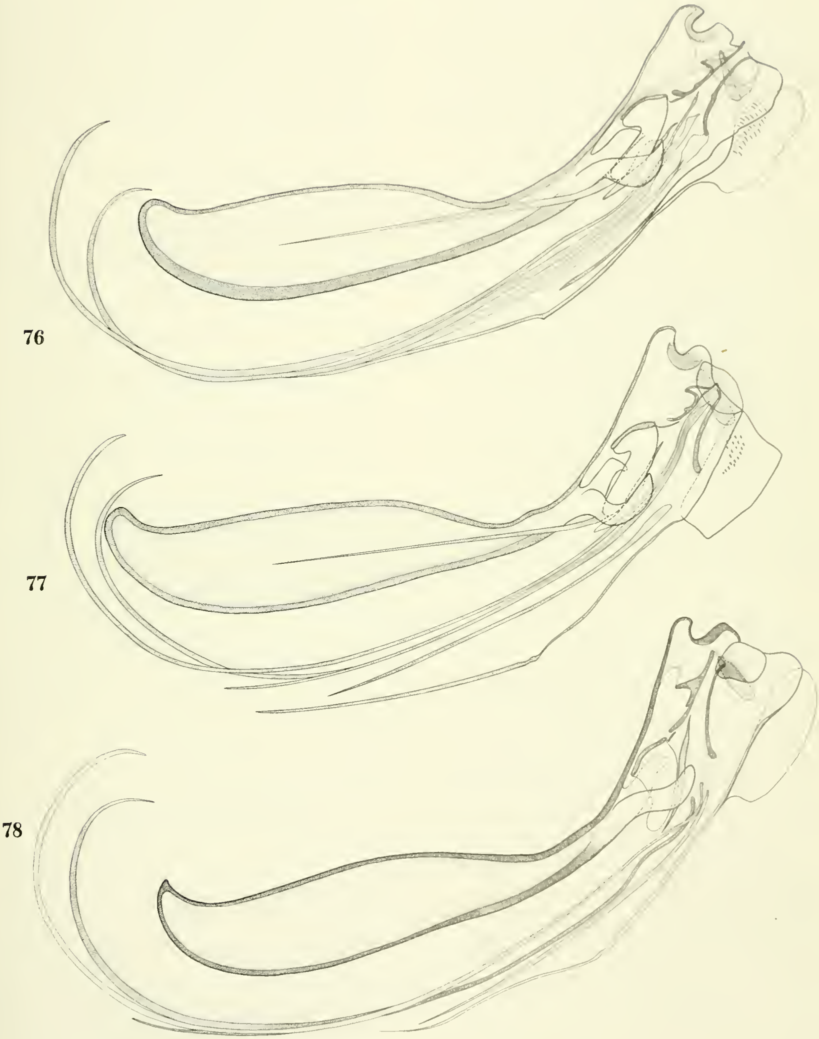
TYPE LOCALITY.— Nicola, British Columbia, Canada.

TYPE SPECIMENS.— Canadian National Collection, Ottawa, Ontario.

DIAGNOSIS.— MALE: *M. spenceri* bears a resemblance to *M. smiti*, *M. sierrae*, and *M. jamesoni*. Only *M. spenceri* has an angular denticle (toothlike process) on the anterior margin of the movable process of the clasper. In addition, one inner fovea of the immovable process of the clasper is more than 50 microns below the dorsal margin of the clas-



Figs. 73–75. Males, aedeagus; 73, *Megarthroglossus divisus* (Ravalli Co., Montana); 74, *M. divisus* (Wayne Co., Utah); 75, *M. wilsoni*.



Figs. 76–78. Males, aedeagus; 76, *Megarthroglossus procus procus* (Whatcom Co., Washington); 77, *M. p. procus* (Washoe Co., Nevada); 78, *M. p. muiri*.

per, and the ventrolateral lobe of sternum VIII is evenly convex.

FEMALE: Both *M. weaveri* and *M. spenceri* have a sinus on the posterior margin of sternum VII and the bulga is not compressed. However, in *M. spenceri* there are 3 antepygidial bristles per side; segment V of the labial palp is less than 300 microns in length and the hilla is less than 40 microns in width.

DISTRIBUTION.— CALIFORNIA: Siskiyou County. CANADA: British Columbia.

MATERIAL EXAMINED.— CALIFORNIA: (Siskiyou Co.) 1 ♂, 1 ♀, ex *Neotoma cinerea*, Thunderbolt Cave, 8-V-1975, Nelson and Smith.

DISCUSSION.— *Megarthroglossus spenceri* has been collected in British Columbia and California from *Neotoma cinerea*. The distribution of this flea is undoubtedly greater than that indicated by existing records. *Megarthroglossus pygmaeus*, described by Wagner (1936), was reduced to the status of a junior synonym of *M. spenceri* by Holland (1976) after he examined male and female specimens collected from Siskiyou Co., California, by Nelson and Smith. As the first revisor, Holland (1949) selected *spenceri* as the valid name because it has line priority over *pygmaeus*.

### *Megarthroglossus weaveri* Eads & Campos

Figs. 46, 58, 71, 95, 101

*Megarthroglossus weaveri* Eads and Campos, 1977.

TYPE HOST.— Not designated (probably *Neotoma mexicana*).

TYPE LOCALITY.— Weaver Ranch, Larimer County, Colorado, at elevations of 1696–1768 meters.

TYPE SPECIMENS.— United States National Museum, Washington, D.C.

DIAGNOSIS.— MALE: *Megarthroglossus weaveri* resembles *M. bisetis* in that both usually possess 2 antepygidial bristles per side and the posterior margin of sternum VIII is evenly convex. However, in *M. weaveri* the inner fovea of the immovable process is greater than 35 microns below the dorsal margin; segment V of the labial palp is more than 220 microns in length; the spur of the crochet is less than 10 microns; the movable process of the clasper is more than 120 microns in length; and metatarsal segment 1 is more than 220 microns in length.

FEMALE: *M. weaveri* and *M. spenceri* resemble each other in that both have a sinus in the posterior margin of sternum VII, and the bulga is not compressed. In *M. weaveri* there are two antepygidial bristles per side, segment V of the labial palp is less than 300 microns in length, and the hilla is less than 40 microns in width.

DISTRIBUTION.— COLORADO: El Paso and Larimer counties.

MATERIAL EXAMINED.— COLORADO: (El Paso Co.) 1 ♂, 1 ♀, ex *Neotoma mexicana*, Fort Carson, 7-X-1977, USAEHA; 1 ♂, same host, same location, 8-X-1977, USAEHA; 1 ♂, same host, same location, 12-X-1977, USAEHA; 1 ♂, same host, same location, 13-X-1977, USAEHA; 1 ♂, 4 ♀, same host, same location, 14-X-1977, USAEHA; 2 ♂, 1 ♀, same host, same location, 16-X-1977, USAEHA; (Larimer Co.) 1 ♀, paratype, ex *Neotoma mexicana*, Weaver Ranch, 30-X-1973, Campos (CDC); 1 ♂, paratype, same host, same location, 25-XI-1974, Campos (CDC).

DISCUSSION.— *Megarthroglossus weaveri* has been collected in El Paso and Larimer counties, Colorado, from *Neotoma mexicana* and *Peromyscus maniculatus*. *Megarthroglossus wilsoni* has been collected from the same locations as *M. weaveri*. Additional collections are needed to clarify host associations and the ecological and taxonomic relationships between *M. wilsoni* and *M. weaveri*.

### *Megarthroglossus wilsoni* Mendez & Haas

Figs. 43, 55, 75, 96, 100

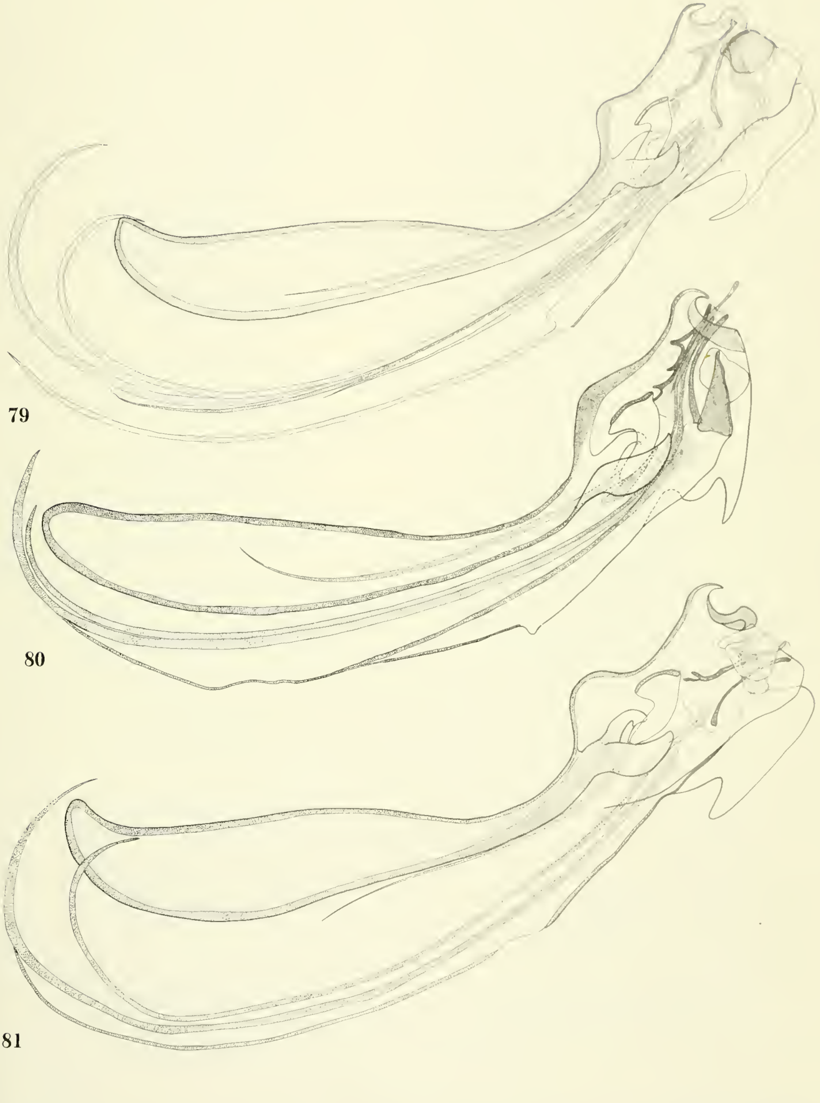
*Megarthroglossus wilsoni* Mendez and Haas 1973: 1132.

TYPE HOST.— *Peromyscus* sp. and *P. maniculatus*.

TYPE LOCALITY.— Brigham Hills, Larimer Co., Colorado.

TYPE SPECIMENS.— United States National Museum, Washington, D.C.

DIAGNOSIS.— MALE: *Megarthroglossus wilsoni* and *M. divisus* are similar, but *M. wilsoni* is different from all other *Megarthroglossus* males in possessing a long inner fovea on the immovable process. *Megarthroglossus wilsoni* may be further separated from *M. di-*



Figs. 79–81. Males, aedeagus; 79, *Megarthroglossus smiti*; 80, *M. spenceri*; 81, *M. sicamus*.

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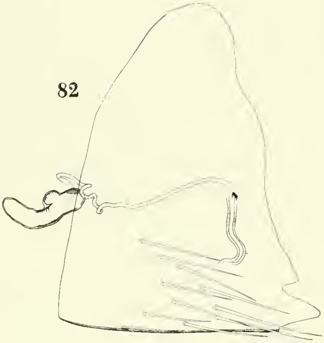

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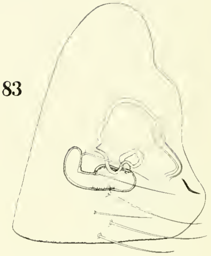

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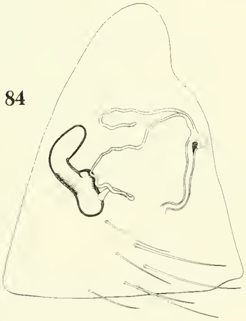

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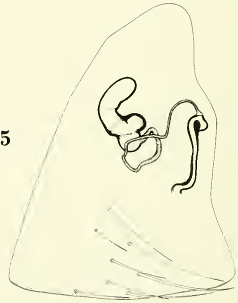

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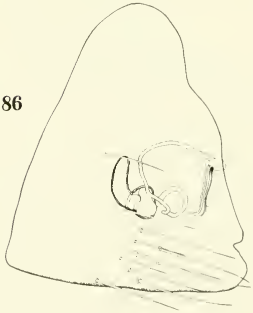

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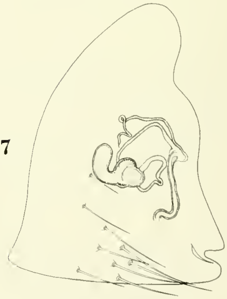
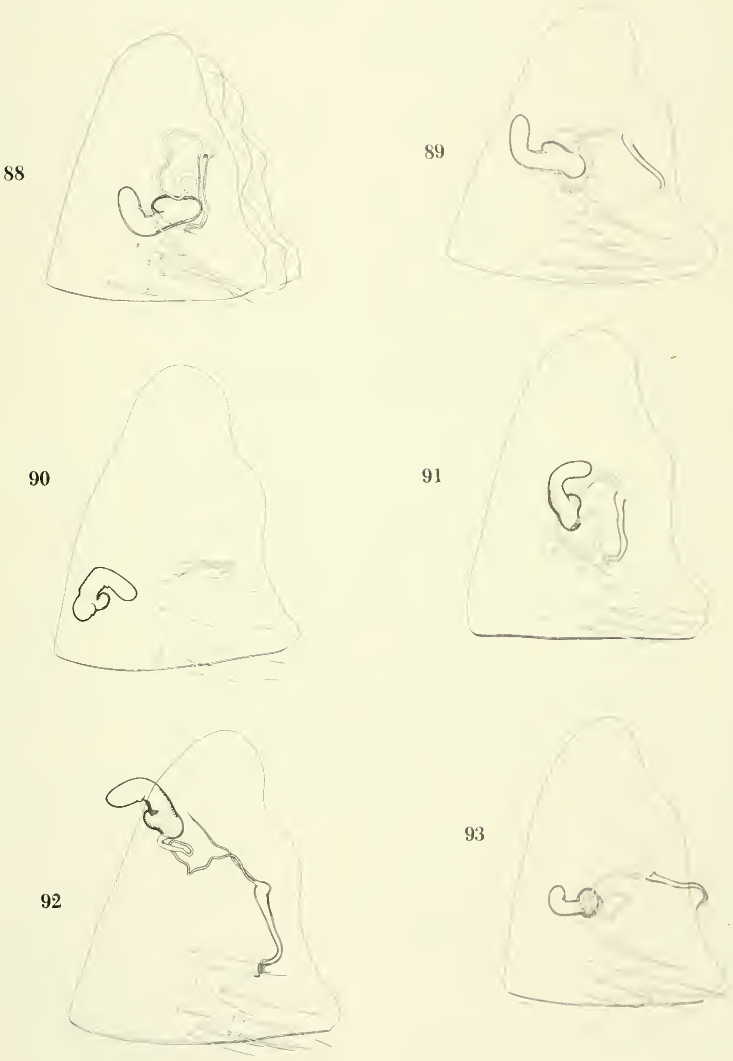
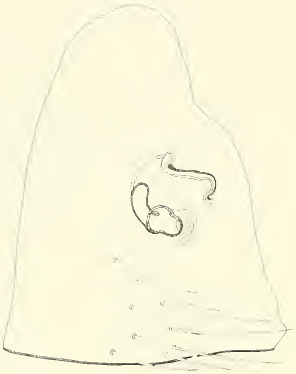


Figs. 82–87. Females, sternum VII; 82, *Megarthroglossus becki*; 83, *M. cavernicolus*; 84, *M. jamesoni*; 85, *M. bisetis*; 86, *M. divisus* (Wayne Co., Utah); 87, *M. divisus* (Ravalli Co., Montana).



Figs. 88–93. Females, sternum VII; 88, *Megarthroglossus procus procus* (Whatcom Co., Washington); 89, *M. p. procus* (Eldorado Co., California); 90, *M. p. muiri*; 91, *M. sicamus*; 92, *M. sierrae*, 93, *M. smiti*

94



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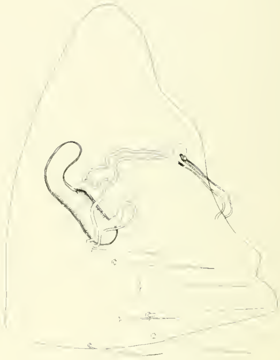

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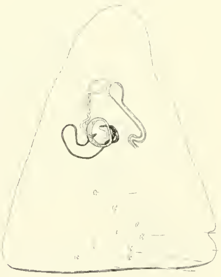

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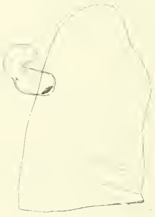

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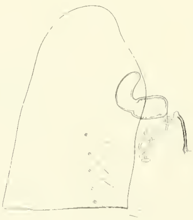

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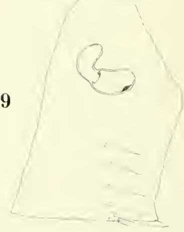


Figs. 94–99. Females, sternum VII; 94, *Megarthroglossus spenceri*; 95, *M. weaveri*; 96, *M. wilsoni*; 97, *Callistopsyllus terinus deuterus*; 98, *C. t. campestris*; 99, *C. t. terinus*.

*visus* in that the inner fovea of the immovable process is more than 40 microns below the dorsal margin, the crochet spur is more than 60 microns in length, and segment V of the labial palp is less than 170 microns in length.

FEMALE: *M. wilsoni* resembles *M. divisus* and *M. becki*. In *M. wilsoni* the sternum VII sinus depth to width ratio is less than 2.40; segment V of the labial palp is less than 260 microns (average length). There are seven spines per side in the pronotal comb, the hilla is less than 35 microns in width, the hilla ratio exceeds 1.20, and the bulga ratio exceeds 1.80.

DISTRIBUTION.— COLORADO: El Paso and Larimer counties. NEW MEXICO: Colfax County.

MATERIAL EXAMINED.— COLORADO: (El Paso Co.) 1 ♀, ex *Neotoma mexicana*, Fort Carson, 13-X-1977, USAEHA; 1 ♂, ex *Peromyscus maniculatus*, same location, 17-X-1977, USAEHA; (Larimer Co.) 1 ♂, paratype, ex *Peromyscus maniculatus*, College Lake, Fort Collins, 29-X-1971, CDC; 1 ♀, paratype, ex *Peromyscus* sp., Bingham Hills, Fort Collins, 24-X-1969, CDC. NEW MEXICO: (Colfax Co.) 1 ♂, paratype, ex *Eutamias minimus* nest in woodpecker hole in dead aspen, SE Red River Pass, Highway 38, 2925 m, 28-VIII-1971, Haas and Wilson (CDC).

DISCUSSION.— *Megarthroglossus wilsoni* has been collected in El Paso and Larimer counties, Colorado, and Colfax County, New Mexico, from species of *Peromyscus*, *Eutamias*, and *Neotoma*. Again, additional data are required to determine host associations and the taxonomic relationship between *M. weaveri* and *M. wilsoni*.

## STENISTOMERA Rothschild

*Stenistomera* Rothschild 1915:307; Ewing 1929:174; Good 1942:132–133; Jellison and Good 1942:132; Ewing and Fox 1943:73; Hubbard 1947:274–304; Holland 1949b:48, 96; Traub and Tipton 1951:267, 268; Jellison, Locker, and Bacon 1953:186; Hopkins 1957:64–87; Hopkins and Rothschild 1962:249; Holland 1965:1052; Jellison and Glesne 1967:300; Egoscue 1968:138; Traub 1968:375–404; Jellison and Senger 1973:70; Lewis 1974:155.

Rothschild (1915) based the genus *Stenistomera* on *Typhlopsylla alpina* Baker (1895). Good (1942) described *macrodactyla* and considered the two known species sufficiently distinct to warrant division of the genus into two subgenera and consequently he described the subgenus *Miochaeta* to contain *macrodactyla*. These subgenera were distinguished from each other on the basis of the helmet-shaped head in *S. alpina* on which there are several spinelike bristles. Stark (1958) elevated the subgenus *Miochaeta* to generic level on the basis of these characteristics. Egoscue (1968) described a new species, *hubbardi*, which he claimed to be intermediate between *alpina* and *macrodactyla* "and makes recognition of the subgenera erected by Good and the genus *Miochaeta* as proposed by Stark untenable." We concur with the evaluation of Egoscue.

DIAGNOSIS.— *Stenistomera* has a readily discernible interantennal groove. The eye is absent and the labial palp is 4-segmented as in *Callistopsyllus* and *Anomiopsyllus*. However, the latter genus does not have a pronotal comb. The mesocoxa has an incomplete longitudinal break that extends for less than one-half the diagonal distance. *Stenistomera* has a comb of dorsolateral bristles on the mesotibia and *Callistopsyllus* does not. In addition, the bristles of the head are more numerous and prominent in *Stenistomera* than in other genera of the subfamily.

DESCRIPTION.— HEAD: Anterior margin convex, angulate or helmet shaped; numerous stout (spiniform in *alpina*) marginal and submarginal bristles; pores and placoids scattered over frons and occiput, but mostly submarginal. Eye absent. Antenna extremely short. Maxillary lobe reduced, angulate. Maxillary palp 4-segmented, short, extends to midpoint on forecoxa. Labial palp well developed, 4-segmented, extends to apex of forecoxa, apex more or less asymmetrical.

THORAX: Pronotal comb of 16–18 teeth. Lateral metanotal area absent. Pleural arch absent. Metepisternum fused with metasternum. Hind coxa narrow, false combs on mesotibiae, four pairs lateral bristles on fifth tarsal segment.

ABDOMEN: One row of bristles on each abdominal tergum. Three antepygidial bristles in both sexes.

MODIFIED ABDOMINAL SEGMENTS—MALE: Fixed process of clasper not well developed; movable process long, narrow, with sides sub-

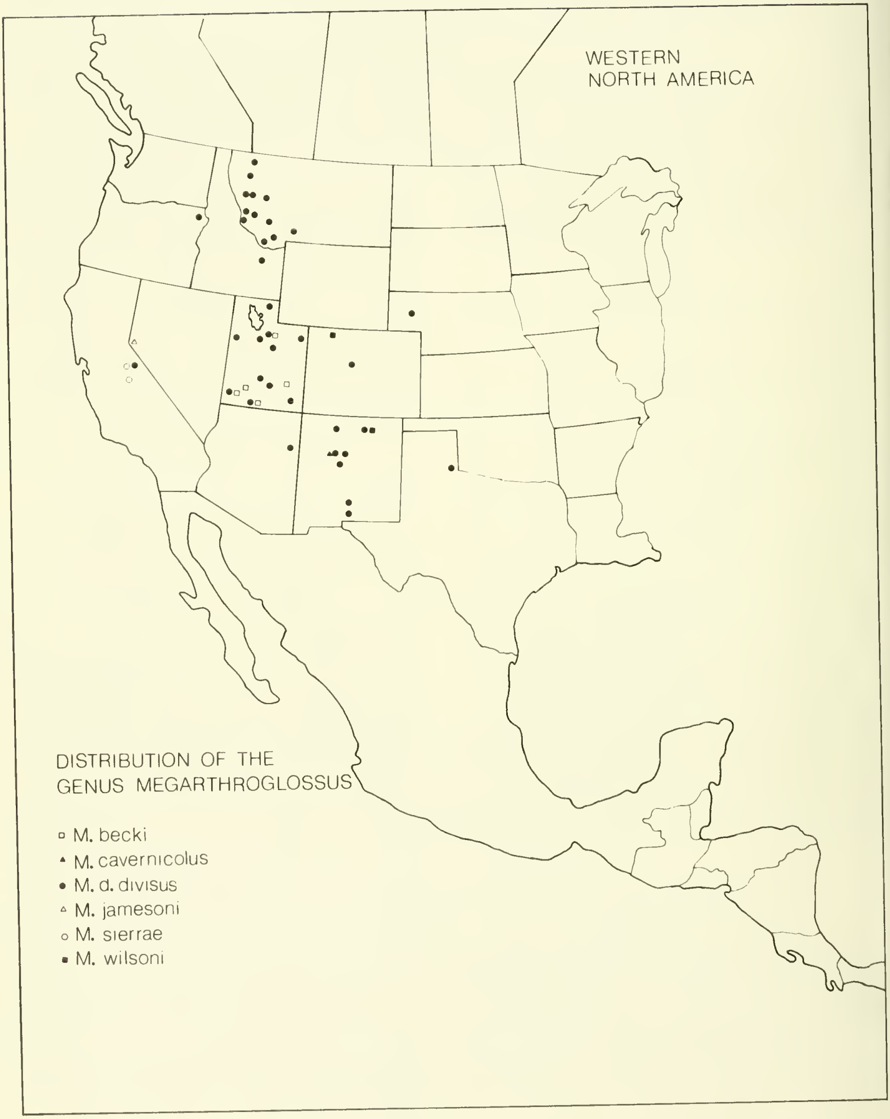

WESTERN
NORTH AMERICA
DISTRIBUTION OF THE
GENUS MEGARTHROGLOSSUS
□ M. becki
▲ M. cavernicolus
● M. d. divisus
△ M. jamesoni
○ M. sierrae
■ M. wilsoni

Fig. 100. Distribution of *Megarthroglossus* species: *M. becki*, *M. cavernicolus*, *M. divisus*, *M. jamesoni*, *M. sierrae*, and *M. wilsoni*.

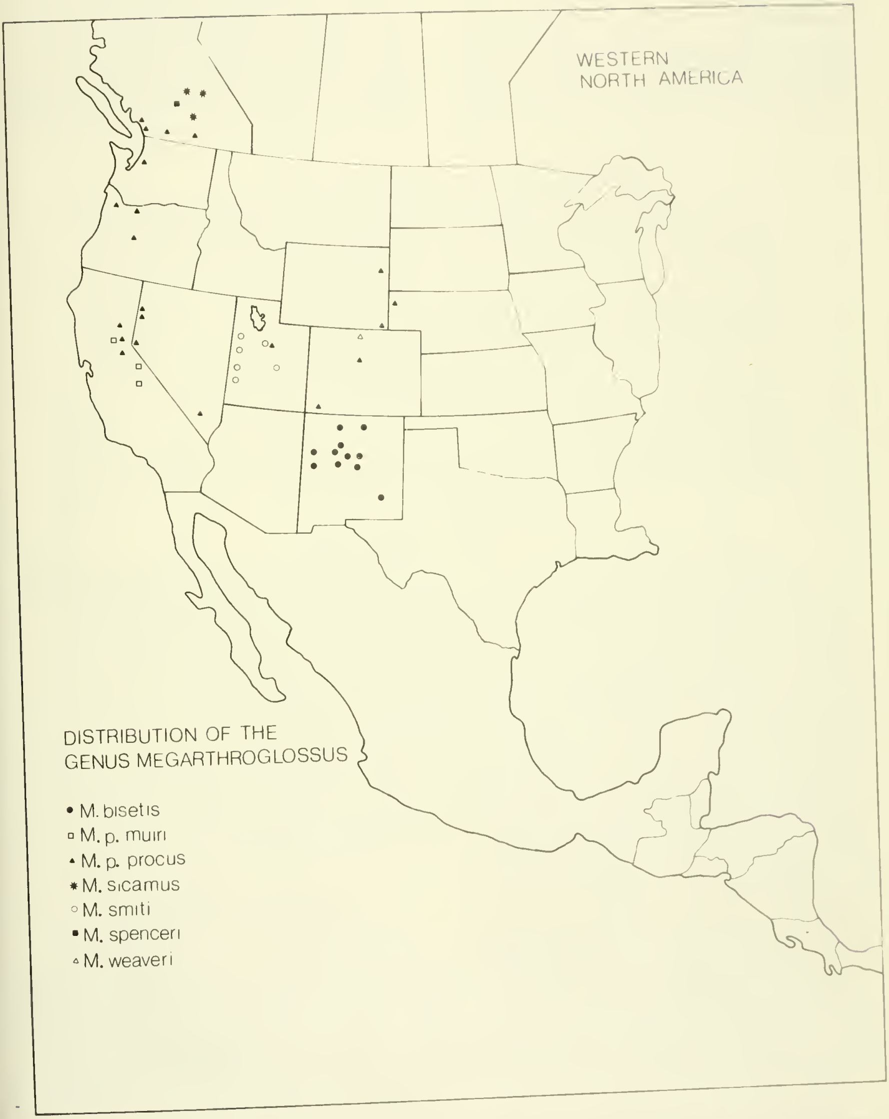

WESTERN NORTH AMERICA
DISTRIBUTION OF THE GENUS MEGARTHROGLOSSUS
● M. bisetis
□ M. p. muiri
▲ M. p. procus
✱ M. sicamus
○ M. smiti
■ M. spenceri
△ M. weaveri

Fig. 101. Distribution of *Megarthroglossus* species: *M. bisetis*, *M. p. muiri*, *M. p. procus*, *M. sicamus*, *M. smiti*, *M. spenceri*, and *M. weaveri*.

parallel, apex truncate; with two well-pigmented, spiniform, apical or subapical setae. Sternum IX with narrow proximal arm but with subapical portion swollen; distal arm expanded, bearing subapical spiniform(s) plus several small marginal and submarginal setae. Aedeagus with narrow, saberlike apodeme, with long-coiled appendage; apodemal rods long, coiled. Crescent sclerite and capsule prominent. Median dorsal lobe well sclerotized, apex somewhat hooklike.

MODIFIED ABDOMINAL SEGMENTS—FEMALE: Posterior margin of sternum VII convex dorsally, with ventral sinus. Bulga of spermatheca barrel shaped; hilla bent at right angles to bulga.

### Key to the Species of *Stenistomera* (Male)

1. Process of clasper broader than distal arm of sternum IX at its widest point (Fig. 107); two spiniform bristles on caudal margin separated by more than 3 times length of one spiniform; distal arm of sternum IX with apex subacuminate (Fig. 104) .......... *macrodactyla*

— Process of clasper narrower than distal arm of sternum IX at its widest point; two spiniform bristles on caudal margin separated by less than 3 times length of one spiniform, distal arm of sternum IX with apex subacuminate to subtruncate .......... 2

2(1). Distal arm of sternum IX with two prominent subapical bristles; apex subacuminate (Fig. 105) .......... *hubbardi*

— Distal arm of sternum IX with one prominent subapical bristle; apex subtruncate (Fig. 103) .......... *alpina*

### *Stenistomera hubbardi* Egoscue

Figs. 28, 105, 108, 109, 114, 115

*Stenistomera hubbardi* Egoscue 1968:138–142; Lewis 1974:155.

TYPE HOST.— *Peromyscus maniculatus* ssp.

TYPE LOCALITY.— Crane, Harney Co., Oregon.

TYPE SPECIMENS.— United States National Museum, Washington, D.C.

DIAGNOSIS.— The labial palp extends for three-fourths the length of the procoxa and the maxillary lobe is subacuminate. The preantennal bristles are larger and heavier than in S. *macrodactyla*, but less so than in S. *alpina*.

DESCRIPTION.— MALE: Movable process of clasper elongate, rectangular, curved slightly caudad, distal one-third with two spiniforms on caudal margin. Base of acetabular bristle midway between sensilial plate and articulation of movable process of clasper. Distal portion of sternum IX blade shaped, with two thick, blunt, subapical bristles.

FEMALE: Three antepygidial bristles approximately equal in length; anal stylet long, about four times longer than wide, with long subapical bristle plus shorter apical bristle. Bulga of spermatheca not markedly dissimilar in shape from that of other members in genus or in *Callistopsyllus terinus*; hilla sharply bent (approximately 90 degrees) shortly after exiting from bulga, apex with prominent sclerotized papilla.

DISTRIBUTION.— OREGON: Harney County.

MATERIAL EXAMINED.— OREGON: (Harney Co.) 1 ♂, 1 ♀ and 1 broken specimen, ex *Peromyscus maniculatus*, 8.0 km south of Crane, 23-X-1966, H. J. Egoscue.

### *Stenistomera macrodactyla* Good

Figs. 29, 104, 107, 110, 113, 115

*Stenistomera macrodactyla* Good 1943:135; Hubbard 1947:306; Jellison, Locker, and Bacon 1953:186; Holdenried and Morlan 1955:133–137; Morlan 1955:93–125; Wiseman 1955:1–18; Parker and Howell 1959:597–604; Hopkins and Rothschild 1962:353–354; Beck 1966:77; Jellison and Glesne 1969:302; Allred 1968:78; Egoscue 1968:140; Tipton and Saunders 1971:18; Haas et al. 1973:282; Pratt and Stark 1973:11; Lewis 1974:155; Egoscue 1976:476.

*Miochaeta macrodactyla* Stark 1959:104.

TYPE HOST.— *Peromyscus eremicus*.

TYPE LOCALITY.— Mojave Co., Arizona.

TYPE SPECIMENS.— United States Public Health Service Plague Laboratory, San Francisco, California.

DIAGNOSIS.— Labial palp extends to apex of the procoxa. Maxillary lobe is subacuminate, but broader at the apex than in S. *hubbardi*. The preantennal bristles are not enlarged or heavily pigmented as in S. *hubbardi* or S. *alpina*.

TABLE 7. Distribution of species of *Stenistomera*.

| AREA | *S. alpina* | *S. hubbardi* | *S. macrodactyla* |
|---|---|---|---|
| Arizona | X | | |
| Colorado | X | | X |
| Idaho | X | | X |
| Montana | X | | |
| Nevada | X | | X |
| New Mexico | X | | X |
| Oregon | X | X | |
| Utah | X | | X |
| Wyoming | X | | X |
| British Columbia | X | | |

TABLE 8. Host associations of the genus *Stenistomera*.

| Host species | *S. alpina* | *S. hubbardi* | *S. macrodactyla* |
|---|---|---|---|
| *Ammospermophilus leucurus* | X | | |
| *Lynx rufus pallescens* | X | | |
| *Neotoma albigula* | X | | |
| *Neotoma albigula albigula* | X | | |
| *Neotoma cinerea* | X | | X |
| *Neotoma cinerea acraia* | X | | |
| *Neotoma cinerea alticola* | X | | |
| *Neotoma lepida* | X | | |
| *Neotoma lepida lepida* | X | | |
| *Neotoma lepida nevadensis* | X | | |
| *Neotoma mexicana* | X | | |
| *Peromyscus crinitus* | X | | X |
| *Peromyscus crinitus pergracilis* | X | | |
| *Peromyscus maniculatus* | | X | X |
| *Peromyscus maniculatus sonoriensis* | X | | |
| *Reithrodontomys megalotis megalotis* | X | | |
| *Urocyon cinereoargenteus* | X | | |
| *Spilogale putorius sayatilis* | X | | |

DESCRIPTION.— MALE: Movable process of clasper elongate, urn shaped, not curved caudad as in S. *hubbardi* or S. *alpina*, with two widely separated spiniforms on caudomesal surface. Base of acetabular bristle near articulation of movable process of clasper. Distal arm of sternum IX narrow at apex, with single thick, blunt subapical bristle.

FEMALE: Three antepygidial bristles of about equal length. Anal stylet long, (about three to four times as long as wide), with row of four ventral marginal bristles of about equal length (variable, usually two to five), one long subapical bristle, plus one short apical bristle. Caudal margin of sternum VII with dorsal portion evenly convex, short subacuminate to triangular ventral lobe ventral to broad, shallow sinus. Bulga typically shaped; hilla evenly curved dorsad, lacks sclerotized papilla as in S. *hubbardi*.

DISTRIBUTION.— COLORADO: Montezuma County. IDAHO: Bingham and Butte counties. NEVADA: Washoe County. NEW MEXICO: Sandoval County. UTAH: Daggett, Iron, San Juan, Tooele, and Uintah counties. WYOMING: Sweetwater County.

MATERIAL EXAMINED.— COLORADO: (Montezuma Co.) 1 ♂, 3 ♀, ex *Peromyscus maniculatus*, Mesa Verde National Park, 26-V-1962, C. Douglas (BYU). IDAHO: (Bingham Co.) 1 ♀, ex *Peromyscus maniculatus*, AEC-NRTS (19Y), 22-IX-1966 (BYU); 3 ♀, same host, AEC-NRTS (21-S), 18-IX-1966 (BYU); 1 ♀, same host AEC-NRTS (21S), 20-XI-1966 (BYU); 1 ♂, 2 ♀, same host, AEC-NRTS (33Y), 17-XI-1967 (BYU); 1 ♂, 1 ♀, ex rodent nest, same location, same date (BYU); 14 ♂, 5 ♀, ex *Peromyscus maniculatus*, AEC-NRTS (33Y), 19-XI-1967 (BYU); 1 ♂, ex *Neotoma cinerea*, AEC-NRTS (33Y), 22-VIII-1967 (BYU); (Butte Co.) 3 ♀, ex *Peromyscus maniculatus*, AEC-NRTS (31Y), 16-I-1967 (BYU); 1 ♂, same host, AEC-NRTS (32Y) 17-XI-1967 (BYU). UTAH: (Daggett Co.) 1 ♂, 1 ♀, ex *Peromyscus maniculatus*, Linwood, 14-VII-1954, C. L. Hayward (BYU); (Iron Co.) 1 ♂, same host, Parowan, 4-IX-1951, Beck and Allred (BYU); (San Juan Co.) 2 ♀, same host, Bluff, 5-V-1951, D. E. Beck (BYU), 1 ♀, same host, Montezuma Creek, 7-VI-1955, Beck et al. (BYU); (Uintah Co.) 1 ♂, 1 ♀, ex *Peromyscus crinitus*, Jensen, 8-XI-1952, Beck and Beck (BYU).

### *Stenistomera alpina* (Baker)

Figs. 30, 38, 102, 103, 106, 111, 112, 115

*Typhlopsylla alpina* Baker 1895:189, 191.

*Ctenopsylla alpina* Wagner 1898:577–578.

*Ctenopsyllus alpinus* Baker 1904:427, 452; Triaboschi 1904:285.

*Stenistomera alpina* Rothschild 1915:307; C. Fox 1925:127; Wagner 1930:144; Stanford 1931:153; Wagner 1939:32; Eskey and Haas 1940:29, 74; Good 1942:133; Jellison and Good 1942:132; Ewing and Fox 1943:73; Hubbard 1943:1–12; Jellison, Khols, and Mills 1943: 1–22; Stanford 1944:175; Hubbard 1947:305; Hubbard 1949:121; Tipton 1950:65; Traub and Hoff 1951:23 pp.; Holland 1952:65–73; Wehrle 1953:37–41; Jellison, Locker, and Bacon 1953:186–187; Augustson 1955:36–39; Morlan 1955:93–125; Wiseman 1955:1–23; Holdenried and Morlan 1956:369–381; Finley 1958:213–552; Parker and Howell 1959:597–604; Stark 1959:103; Hopkins and Rothschild 1962:350–353; Beck and Allred 1966:13; Jellison and Glesne 1967:300–301; Allred 1968:78; Egoscue 1968:140; Tipton and Saunders 1971:18; Pratt and Stark 1973:11; Haas et al. 1973:282; Jellison and Senger 1973:71; Lewis 1974:155; Egoscue 1976:475–488.

*Delotelis mohavensis* Augustson 1942:138; Auguston 1943:86.

TYPE HOST.— Mountain rat (probably *Neotoma cinerea*).

TYPE LOCALITY.— Georgetown, Clear Creek Co., Colorado.

TYPE SPECIMENS.— United States National Museum, Washington, D.C.

DIAGNOSIS.— Labial palp extends beyond the apex of the procoxa and usually beyond the trochanter; the maxillary lobe is acuminate and the preantennal bristles are thick and heavily pigmented; some are spiniformlike.

DESCRIPTION.— MALE: Movable process of clasper elongate, curved slightly caudad, with two closely spaced spiniforms on mesocaudal margin, similar to that of *S. hubbardi*. Base of acetabular bristle displaced toward sensilial plate as in *S. hubbardi*, but less so than in *S. macrodactyla*. Distal arm of sternum IX somewhat similar to *S. hubbardi*, but with single, thick, blunt bristle to caudoventral angle, apex subtruncate.

FEMALE: Three antepygidial bristles, middle bristle longest. Anal stylet long, three to four times as long as wide, usually with two ventral bristles, one long subapical bristle plus short apical bristle. Bulga typical, but with a slight narrowing at end near hilla; no sclerotized papilla on hilla.

DISTRIBUTION.— ARIZONA: Apache, Cochise, and Coconino counties. COLORADO: Clear Creek and El Paso counties. IDAHO: Butte County. MONTANA: Custer, Madison, and Ra-

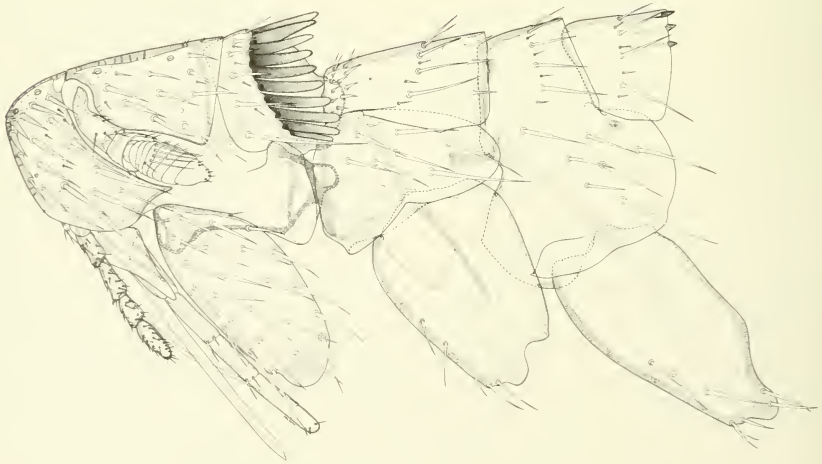


Fig. 102. *Stenistomera alpina* (Baker): Male, head and thorax including coxae.

valli counties. Nevada: Nye and Washoe counties. New Mexico: Chaves, Bernalillo, and Sandoval counties. Oregon: Harney County. Utah: Cache, Kane, Juab, Salt Lake, San Juan, Sanpete, Sevier, Tooele, and Utah counties. Wyoming: Albany and Sweetwater counties. Canada: Alberta.

Material examined.— Arizona: (Cochise Co.) 1 ♀, ex *Neotoma mexicana*, 0.8 km E Buena Vista Park., Chiricahua Mts., 23-XI-1957, C. E. Ordway (BYU). Idaho: (Butte Co.) 7 ♂, 5 ♀, ex *Neotoma cinerea*, AEC-NRTS (29), 15-XII-1966 (BYU). Nevada: (Nye Co.) 1 ♂, 3 ♀, ex *Peromyscus crinitus*, Mercury, AEC-NRTS, 6-XII-1961 (BYU); 1 ♂, 5 ♀, ex *Neotoma lepida*, same location, 11-XII-1960 (BYU); 2 ♂, 11 ♀, same host, same location, 9-XII-1961 (BYU); 6 ♂, 19 ♀, same host, same location, 11-XII-1961 (BYU); 1 ♂, 3 ♀, same host, same location, 8-XI-1961 (BYU); 2 ♂, 2 ♀, ex *Neotoma albigula*, same location, 28-X-1961 (BYU); 13 ♂, 35 ♀, ex *Neotoma lepida*, same location, 6-XII-1961 (BYU); 1 ♂, ex *Ammospermophilus leucurus*, same location, 7-XII-1961; 1 ♀, ex *Neotoma lepida*, same location, 16-XI-1961 (BYU); 1 ♂, 2 ♀, same host, same location, 11-XI-1961 (BYU); 22 ♂, 37 ♀, same host, same location, 17-XII-1961 (BYU); 1 ♂, 2 ♀, same host, same location, 5-I-1962 (BYU); 4 ♂, 11 ♀, same host, same location, 20-XII-1961 (BYU); 1 ♂, same host, same location, 7-I-1962 (BYU); 1 ♂, same host, same location, 2-I-1962 (BYU); 1 ♂, same host, same location, 2-I-1962 (BYU); 7 ♂, 13 ♀, same host, same location, 17-XII-1961 (BYU); 1 ♂, 1 ♀, ex *Neotoma lepida lepida*, Beatty, 27-XII-1947, C. A. Hubbard (BYU); 27-XII-1947, C. A. Hubbard (BYU). New Mexico: (Bernalillo Co.) 1 ♂, 1 ♀, ex *Neotoma a. albigula*, 28.8 km E Albuquerque, 6-III-1949, H. H. Lewis (BYU). Utah: (Kane Co.) 1 ♂, 2 ♀, ex *Urocyon cinereoargenteus*, NAV-KAI, 14-XI-1971 (BYU); 1 ♀, ex *Peromyscus crinitus*, same location, 11-XII-1971 (BYU); (Juab Co.) 8 ♂, 24 ♀, ex *Neotoma lepida lepida*, Topaz Mt., 19-I-1964 (Egoscue); 5 ♂, 12 ♀, same host, same location, 20-I-1964 (Egoscue); 4 ♂, 13 ♀, same host, Fish Springs, 1-XII-1964 (Egoscue); 1 ♂, ex *Reithrodontomys megalotis megalotis*, same location, 1-XII-1964 (Egoscue); 1 ♀, ex *Peromyscus maniculatus sonoriensis*, Callao, 26-I-1965 (Egoscue); (San Juan Co.) 2 ♂, ex *Neotoma cinerea*, S Moab, 8-V-1951, Allred and Myklebust (BYU); (Tooele Co.) 2 ♂, 1 ♀, ex *Lynx rufus pallescens*, 9.6 km E Granite Mt., 1300 m. 5-III-1965, H. J. Egoscue (Egoscue); 1 ♂, ex *Neotoma lepida lepida*, granite outcrops, E Granite Mt., 1380 m 19-XI-1965, H. J. Egoscue (Egoscue); 5 ♂, same host, same location, same elevation, 13-I-1966, H. J. Egoscue (Egoscue); 2 ♂, 5 ♀, same host, same location, same elevation, 18-I-1966, H. J. Egoscue (Egoscue); 5 ♂, 8 ♀, same host, same location, same elevation, 24-III-1966, H. J. Egoscue (Egoscue); 6 ♀, same host, same location, same elevation, 9-III-1966, H. J. Egoscue (Egoscue); 3 ♂, same host, same location, same elevation, 15-III-1966; H. J. Egoscue (Egoscue); 4 ♀, 2 ♂, same host, same location, same elevation, 25-II-1966, H. J. Egoscue (Egoscue); 2 ♂, same host, same location, same elevation, 2-III-1966; H. J. Egoscue (Egoscue); 1 ♂, same host, same location, same elevation, 19-XI-1965, H. J. Egoscue (Egoscue); 1 ♂, same host, same location, same elevation, 19-II-1966, H. J. Egoscue (Egoscue); 1 ♂, 3 ♀, same host, same location, same elevation, 17-II-1966, H. J. Egoscue (Egoscue); 1 ♂, 1 ♀, same host, same location, same elevation, 17-XI-1965, H. J. Egoscue (Egoscue); 1 ♂, 3 ♀, same host, same location, same elevation, 13-I-1966, H. J. Egoscue (Egoscue); 2 ♂, 1 ♀, ex *Peromyscus crinitus pergracilis*, same location, same elevation, 12-I-1966, H. J. Egoscue (Egoscue); 1 ♂, same host, same location, same elevation, 16-III-1966, H. J. Egoscue (Egoscue); 1 ♀, same host, same location, same elevation, 18-I-1966, H. J. Egoscue (Egoscue); 1 ♀, same host, same location, same elevation, 11-I-1966, H. J. Egoscue (Egoscue); 1 ♂, 2 ♀, ex *Spilogale putorius sayatilis*, same location, same elevation, 19-I-1966, H. J. Egoscue (Egoscue); 1 ♂, 6 ♀, ex *Peromyscus crinitus pergracilis*, Little Granite Mt., 1440 m, 6-XII-1961, H. J. Egoscue (Egoscue); 1 ♂, 2 ♀, ex *Neotoma lepida lepida*, same location, same elevation, 6-XII-1966, H. J. Egoscue (Egoscue); 1 ♂, 2 ♀, same host, same location, same elevation, 8-XII-1966, H. J. Egoscue (Egoscue); 1 ♂, 1 ♀, same host, same location, same elevation, 14-XII-1966, H. J. Egoscue (Egoscue); 8 ♂, 7 ♀, same host, same location, same elevation, 15-XII-

1966, H. J. Egoscue (Egoscue); 1 ♂, 2 ♀, same host, same location, same elevation, 20-XII-1966, H. J. Egoscue (Egoscue); 4 ♂, 4 ♀, same host, same location, same elevation, 21-XII-1966, H. J. Egoscue (Egoscue); 4 ♂, 10 ♀, same host, same location, same elevation, 6-I-1967, H. J. Egoscue (Egoscue); 5 ♂, 4 ♀, same host, same location, same elevation, 25-I-1967, H. J. Egoscue (Egoscue); 1 ♀, ex *Peromyscus maniculatus sonoriensis*, Johnson Pass, 1797 m, 11-III-1969, H. J. Egoscue (Egoscue); 1 ♂, same host, Wendover, 12-XII-1964 (Egoscue); 1 ♀, same host, Lakeside Mts., 16-III-1965 (Egoscue); 2 ♂, 2 ♀, *Neotoma lepida lepida*, Johnson Pass, 1872 m, 23-I-1969, H. J. Egoscue (Egoscue); 1 ♀, same host, Little Granite Mt., 1418 m, 31-I-1963, J. G. Bittmenn (Egoscue); 4 ♀, same host, Wendover, 12-XII-1964 (Egoscue); 1 ♂, 1 ♀, same host, Grassy Mt., 1590 m, 30-XI-1967, H. J. Egoscue (Egoscue); 1 ♂, 2 ♀, same host, W Stansbury Island, 1302 m. 29-II-1968, H. J. Egoscue (Egoscue); 1 ♀, ex *Neotoma c. acraia*, Johnson Pass, 1830 m, 22-I-1969, H. J. Egoscue (Egoscue); 1 ♂, 1 ♀, ex *Peromyscus crinitus pergracilis*, N. Dugway Mr., 1500 m, 27-II-1967, H. J. Egoscue (Egoscue); (Utah Co.) 1 ♀, ex *Neotoma cinerea* nest, Provo, 18-XI-1948, V. J. Tipson (BYU); 1 ♀, same host, Buckley's Mine, Provo, 24-XI-1949, D. M. Allred (BYU); 1 ♂, 3 ♀, ex *Neotoma cinerea* (dung), Rock Canyon, Provo, 11-III-1949, V. J. Tipton (BYU); 1 ♂, 3 ♀, ex *Neotoma cinerea*, Provo Canyon, Provo, 12-XI-1949, H. Goldschmidt (BYU). OREGON: (Harney Co.) 6 ♂, 27 ♀, ex *Neotoma cinerea alticola*, 11.2 km S Crane, 1290 m. 25-XI-1968, H. J. Egoscue (Egoscue); 2 ♀, ex *Neotoma lepida nevadensis*, 8 km S Crane, 1290 m. 25-XI-1968, H. J. Egoscue (Egoscue).

DISCUSSION.— *Stenistomera alpina* has a greater recorded distribution than the other two species of the genus and it probably occurs in all eleven western states. More than 90 percent of the specimens in our collection were associated with *Neotoma lepida* and most of them were collected during winter months. Although there is some slight variation in the location of the spiniforms on the movable process of the clasper, most of our specimens show little variation in characters of taxonomic importance.

## COLLECTION DATA FOR SPECIMENS USED FOR ILLUSTRATIONS

*Callistopsyllus terinus campestris* Holland: male and female, ex *Peromyscus* sp., Alberta, Canada, 27-V-1949, G. P. Holland (Holland).

*Callistopsyllus terinus deuterus* Jordan: male and female, ex *Peromyscus truei*, 1.6 km S El Condor, Baja California, Mexico, 31-XII-1962, W. J. Wrenn (Traub).

*Callistopsyllus terinus terinus* (Rothschild): male and female, ex *Peromyscus maniculatus*, AEC-NRTS, Idaho, 22-III-1967 collectors unknown (BYU).

*Conorhinopsylla nidicola* Jellison: male and female paratypes, ex *Neotoma* sp. nest, Lawrence, Douglas Co., Kansas, 11-XI-1944, R. H. Beamer (Traub).

*Conorhinopsylla stanfordi* Stewart: male and female, ex *Glaucomys volans*, Otsego Co., New York, 6-XII-1956, P. Connors (Benton).

*Megarthroglossus becki* Tipton and Allred: male and female paratypes, ex *Neotoma cinerea* nest, Buckley's Mine, Provo, Utah Co., Utah, 24-XI-1949, D. M. Allred (BYU).

*Megarthroglossus bisetis* Jordan and Rothschild: male and female, ex *Neotoma micropus*, Red Bluff Ranch, Chaves Co., New Mexico, 25-V-1967, B. Miller (Lewis).

*Megarthroglossus cavernicolus* Mendez and Haas: male and female paratypes, ex *Neotoma cinerea* nest, cave W edge Valle Grande, Jemez Mts., Sandoval Co., New Mexico, 18-IX-1970, G. E. Haas et al. (Mendez).

*Megarthroglossus divisus* (Baker): male and female, ex *Sciurus fremonti* nest, Elkhorn R. S., Wayne Co., Utah, 9-VIII-1952, M. Killpack et al. (BYU).

*Megarthroglossus divisus* Wagner: male and female, ex packrat (*Neotoma* sp.) nest, 8 mi Creek, Ravalli Co., Montana, 29-XII-1962, C. M. Senger (Senger).

*Megarthroglossus jamesoni* Smit: male and female, ex *Neotoma cinerea* nest, Pine Nut Mts., Douglas Co., Nevada, 25-III-1951, E. W. Jameson (Jameson).

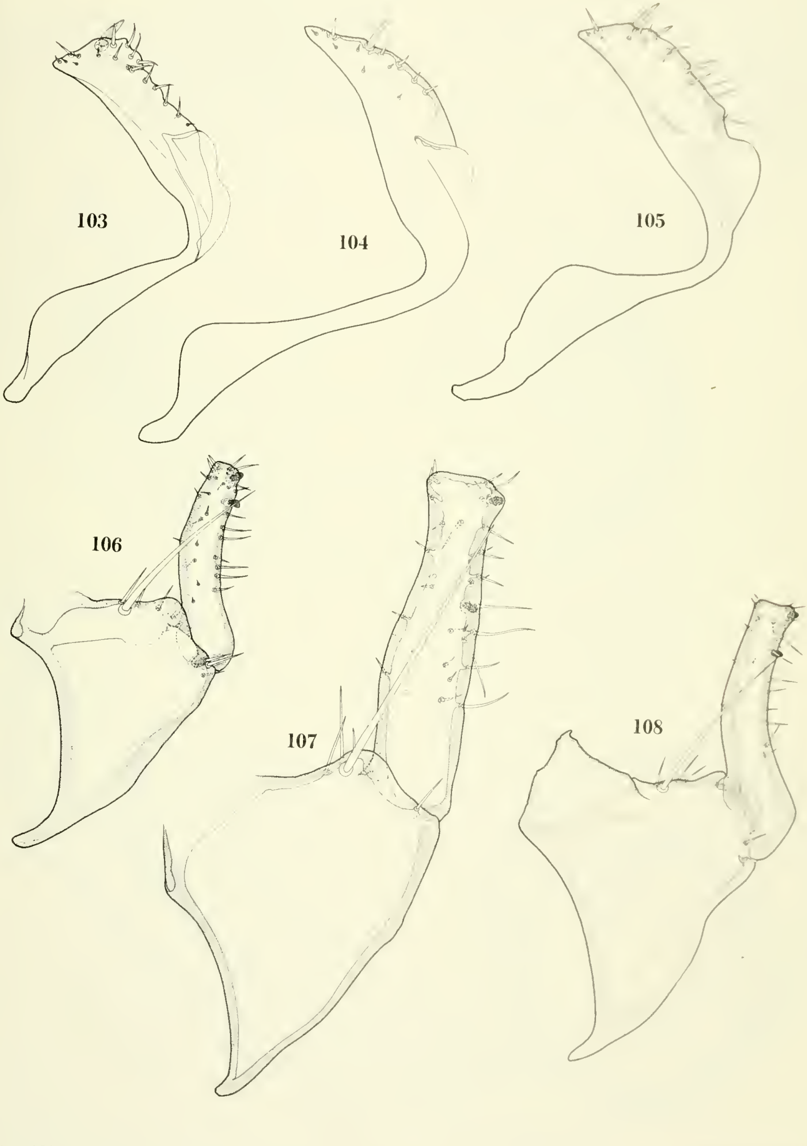
*Megarthroglossus procus procus* Jordan and Rothschild: male and female, ex packrat (*Neotoma* sp.) nest, Glacier, Whatcom Co., Washington, X-1963, C. M. Senger (Senger).

*Megarthroglossus procus procus* Jordan and Rothschild: male ex "chipmunk," Washoe Co., Nevada, X-1936, C. R. Eskey; female ex "chipmunk," Eldorado, California, X-1936, C. R. Eskey.

*Megarthroglossus procus muiri* Augustson: male holotype, ex *Tamiasciurus d. albolimbatus*, Tully's Hole, Fresno Co., California, 25-VIII-1941, G. F. Augustson (Augustson); female allotype, ex *Sorex* (*Neo.*) *navigator*, Tully's Hole, Fresno Co., California, 24-VIII-1941, G. F. Augustson (Augustson).

*Megarthroglossus sicamus* Jordan and Rothschild: male paralectotype, ex *Canis latrans*, Eagle River, Sicamous, British Columbia, Canada, 6-IX-1903, G. F. Dippie (Smit); female ex *Neotoma* sp., Pavilion Lake, British Columbia, Canada, 5-VII-1950, K. B. (Holland).

*Megarthroglossus sierrae* Augustson: male holotype, ex *Ochotona s. muiri*, Cascade Valley, Fresno Co., California, 27-VIII-1941, G. F. Augustson (Augustson); female allotype, ex *Tamiasciurus d. albolimbatus*, Mammoth Lakes, Mono Co., California, 31-VII-1939, G. F. Augustson (Augustson).



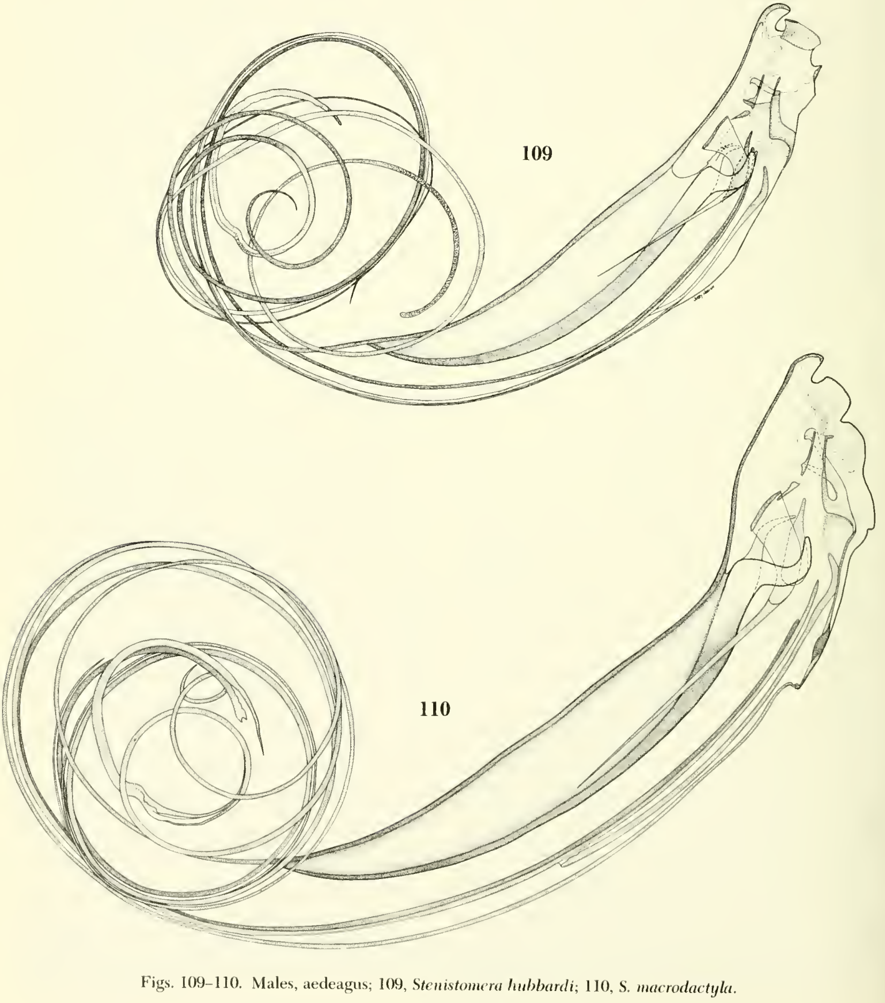
Figs. 103–108. Males, sternum IX; 103, *Stenistomera alpina* ; 104, *S. macrodactyla*; 105, *S. hubbardi*; 106–108, claspers; 106, *S. alpina*; 107, *S macrodactyla*; 108, *S. hubbardi*.

*Megarthroglossus spenceri* Wagner: male holotype (*Megarthroglossus pygmaeus*), ex *Neotoma cinerea occidentalis*, Nicola, British Columbia, Canada, 25-VIII-1932, collector unknown (Holland); female holotype (*Megarthroglossus spenceri*), ex *Ochotona princeps*, Nicola, British Columbia, Canada, 26-VIII-1932, collector unknown (Holland).

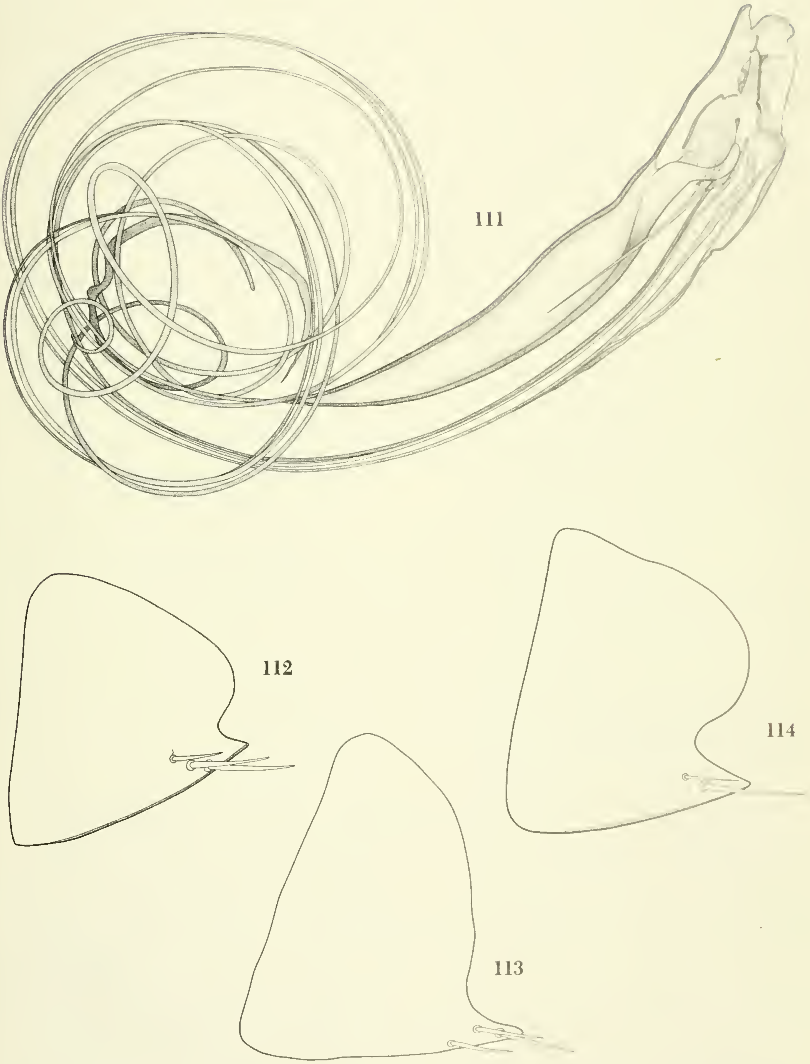
*Megarthroglossus smiti* Mendez: male and female paratypes, ex *Neotoma lepida*, Lynndyl, Millard Co., Utah, 17-XI-1951, Barnum, Moore, Melander and Cloward (BYU).

*Megarthroglossus weaveri* Eads and Campos: male and female paratypes, ex *Neotoma mexicana*, Weaver Ranch, Larimer Co., Colorado, 25-XI-1974 and 30-X-1973 (respectively), E. G. Campos (Eads).

*Megarthroglossus wilsoni* Mendez and Haas: male paratype, ex *Eutamias minimus* nest, 0.8 km SE Red River Pass, Colfax Co., New Mexico, 28-VIII-1971, Haas and Wilson (Mendez); female paratype, ex *Peromyscus maniculatus*, 7.2 km NW Ft. Collins, Larimer Co., Colorado, 29-X-1969, collector unknown (Eads).



Figs. 109–110. Males, aedeagus; 109, *Stenistomera hubbardi*; 110, *S. macrodactyla*.



Figs. 111–114. Males, aedeagus; 111, *Stenistomera alpina*. sternum VIII; 112, *S. alpina*; 113, *S. macrodactyla*, 114 *S. hubbardi*.

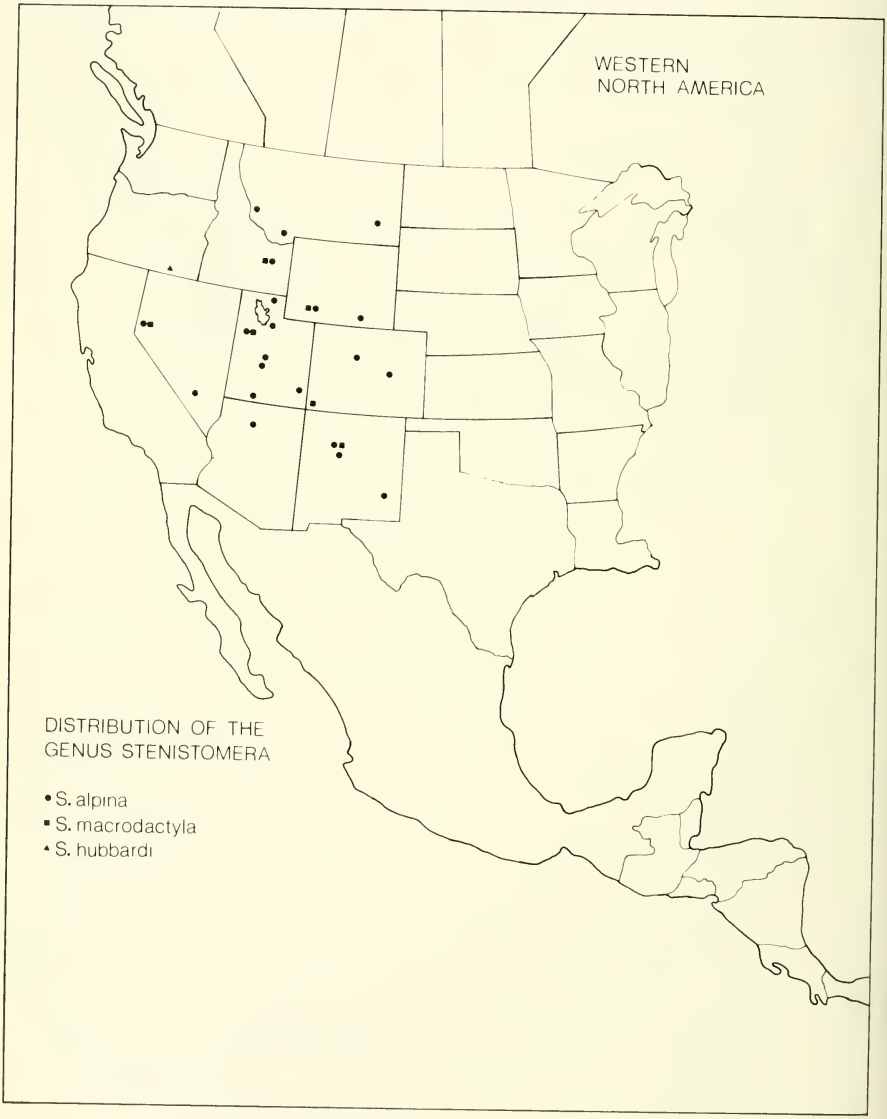

WESTERN NORTH AMERICA
DISTRIBUTION OF THE GENUS STENISTOMERA
• S. alpina
▪ S. macrodactyla
▴ S. hubbardi

Fig. 115. Distribution of *Stenistomera alpina*, *S. hubbardi* and *S. macrodactyla*.

*Stenistomera alpina* (Baker), male and female, ex *Neotoma lepida*, Mercury, AEC-NRTS, Nye County, Nevada, 11-III-1960, collector unknown (BYU).

*Stenistomera hubbardi* Egoscue, male and female, ex *Peromyscus maniculatus*, 8.0 km S at Crane, Harney County, Nevada, 23-X-1966, H.J. Egoscue.

*Stenistomera macrodactyla* Good, male and female, ex *Peromyscus maniculatus*, AEC-NRTS, Bingham County, Idaho, 19-XI-1967, collector unknown (BYU).

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# KARYOTYPES OF FOUR *ARTEMISIA* SPECIES: *A. CARRUTHII, A. FILIFOLIA, A. FRIGIDA,* AND *A. SPINESCENS*[1]

E. Durant McArthur and C. Lorenzo Pope[2]

Abstract.— *Artemisia carruthii* and *A. frigida* of the subgenus Artemisia and *A. filifolia* and *A. spinescens* of the subgenus Dracunculus all have chromosome numbers based on $x = 9$. Diploid ($2n = 18$) karyotypes of each species are composed of large, medium, and small chromosomes that are mainly metacentric and submetacentric. The individual karyotypes are similar but distinctive. *Artemisia filifolia*'s karyotype and chemistry is quite similar to that of Section Tridentatae, but *A. filifolia* has significant morphological differences with respect to the Tridentatae. *Artemisia spinescens* includes a tetraploid ($2n = 36$) population as well as diploid populations. Karyotypic analysis of a tetraploid *A. spinescens* suggests that it is an autotetraploid, thus carrying out a common theme in *Artemisia* (autopolyploidy).

The genus *Artemisia* (Anthemideae, Compositae) is principally a temperate northern hemisphere plant group (Good 1974, Bailey Hortorium Staff 1976). A few of its 250 species, however, extend to South America and southern Africa. Most *Artemisia* phylogenists have suggested an origin for *Artemisia* in Eurasia because of the preponderance of diverse species growing there and because most of its Anthemideae relatives occur there (Stebbins 1974, Cronquist 1978, McArthur and Plummer 1978, McArthur 1979). Beetle (1979) recently suggested an American origin for the genus. Even disallowing Beetle's hypothesis, North America is without question a center of diversity for *Artemisia*. Several *Artemisia* species complexes (Clausen 1951: groups of closely related plants capable of intragroup gene exchange) appear to be evolving in North America (Hall and Clements 1923, Keck 1946, Ward 1953, Beetle 1960, Estes 1969, McArthur and Plummer 1978).

*Artemisia* has chromosome numbers based on $x = 6,7,8$, and 9 (Kawatani and Ohno 1964, Wiens and Richter 1966). By far the most common base number for *Artemisia* is $x = 9$, however, as it is for the whole of the Anthemideae (Persson 1974). Several *Artemisia* species and species complexes are composed of polyploid series. Euploid series based on $x = 9$ are most common (Table 1), but aneuploidy and amphiploidy based on other $x$'s are also known (Suzuka 1950, 1952, Kawatani and Ohno 1964). The euploid complexes may be *auto*polyploid with one basic genome or *allo*polyploid with different genomes (Persson 1974) or somewhere in between—a segmental autopolyploid or allopolyploid (Stebbins 1971), in which case, genomes are partially differentiated.

Our work with *Artemisia* has been mainly with the *A. tridentata* Nutt. complex (=section Tridentatae) (Hanks et al. 1973, McArthur and Plummer 1978, McArthur et al. 1979, Welch and McArthur 1979). To better understand the Tridentatae, we have also looked at sympatric, non-Tridentatae, perennial *Artemisia*. This paper reports first publication of karyotypes of four non-Tridentatae species. Two species represent the subgenus Artemisia (*A. carruthii* Wood and *A. frigida* Willd.) and two represent the subgenus Dracunculus (*A. filifolia* Torr. and *A. spinescens* D. C. Eaton). The third subgenus in *Artemisia* is Seriphidium, which is principally Eurasian and North African. The section Tridentatae has been assigned to Seriphidium, but the Tridentatae are probably independent of and parallel to the Seriphidia (McArthur and Plummer 1978).

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## MATERIALS AND METHODS

PLANT MATERIALS.— The plant materials studied were from the native collection sites and from transplanted wildings at the Snow Field Station in Ephraim, Utah. Each collection was assigned a culture number preceded by *U* to indicate its order of accession. Original locations of plant populations are given in Table 2. Voucher herbarium specimens for each accession have been deposited in the Shrub Sciences Laboratory Herbarium (SSLP).

KARYOTYPING.— Seed was collected from open-pollinated plants at the Snow Field Station for *A. carruthii, A. filifolia,* and *A. frigida,* and from the natural populations for *A. spinescens.* Root tips from seedlings germi-

TABLE 2.— *Artemisia* accessions studied.

| Taxon | Culture | Utah collection site | Elevation (m) |
|---|---|---|---|
| *A. carruthii* | U4 | Clear Creek Canyon, Sevier County | 2,060 |
| *A. filifolia* | U7 | Kanab, Kane County | 1,510 |
| *A. frigida* | U9 | Sunglow Park, Wayne County | 2,070 |
| *A. spinescens* | U3 | Gunnison, Sanpete County | 1,550 |
| *A. spinescens* | U4 | Ouray, Uintah County | 1,420 |

TABLE 1.— Euploid patterns in $x = 9$ *Artemisia*.

| | Number of species[2] with $2n$ chromosomes | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Subgenus[1] | 18 | 27 | 36 | 54 | 72 | 18–36 | 18–45 | 18–54 | 18–72 | 18–90 | 36–54 | References[2] |
| Artemisia | 49 | – | 19 | 6 | – | 8 | – | 2 | – | – | 1 | Keck (1946)<br>Suzaka (1950, 1952)<br>Arano (1962, 1963, 1968)<br>Ehrendorfer (1964)<br>Kawatani and Ohno (1964)<br>Estes (1969)<br>Korobkov (1972) |
| Dracunculus | 9 | – | 13 | 1 | – | 2 | – | – | – | 1 | – | Kawatani and Ohno (1964)<br>Rousi (1968)<br>Filatova (1971)<br>Korobkov (1972)<br>McArthur and Pope (1977) |
| Seriphidium | 15 | 1 | 13 | – | 1 | 3 | 1 | 1 | – | – | 1 | Suzuka (1952)<br>Kawatani and Ohno (1964)<br>Filatova (1974a and 1974b)<br>Persson (1974) |
| Tridentatae[1] | – | – | – | – | – | 8 | – | 1 | 1 | – | – | Ward (1953)<br>Taylor et al. (1964)<br>McArthur and Plummer (1978)<br>McArthur (unpublished) |
| | 73 | 1 | 45 | 7 | 1 | 21 | 1 | 4 | 1 | 1 | 2 | |

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[1] See McArthur and Plummer (1978) and McArthur (1979) for historical development. The section Tridentatae has not been formally proposed as a subgenus, but it is independent of and more or less parallel to the three recognized subgenera.

[2] The references and hence the number of species are not exhaustive, but are representative.

nated in petri dishes were pretreated with colchicine, fixed in 1:3 acetic alcohol, stained in acetocarmine, and squashed on a microscope slide in Hoyer's solution (McArthur and Plummer 1978). Slides are stored at the Shrub Sciences Laboratory.

Several seedlings of each accession were checked for chromosome number (McArthur and Pope 1977), but karyotypes were prepared from one slide per accession a slide with flat photogenic cells. Five randomly selected metaphase plates from each slide were photomicrographed (Fig. 1). Prints at a magnification of 3120X were used to prepare the karyotypes in a manner slightly modified from that outlined in our earlier paper

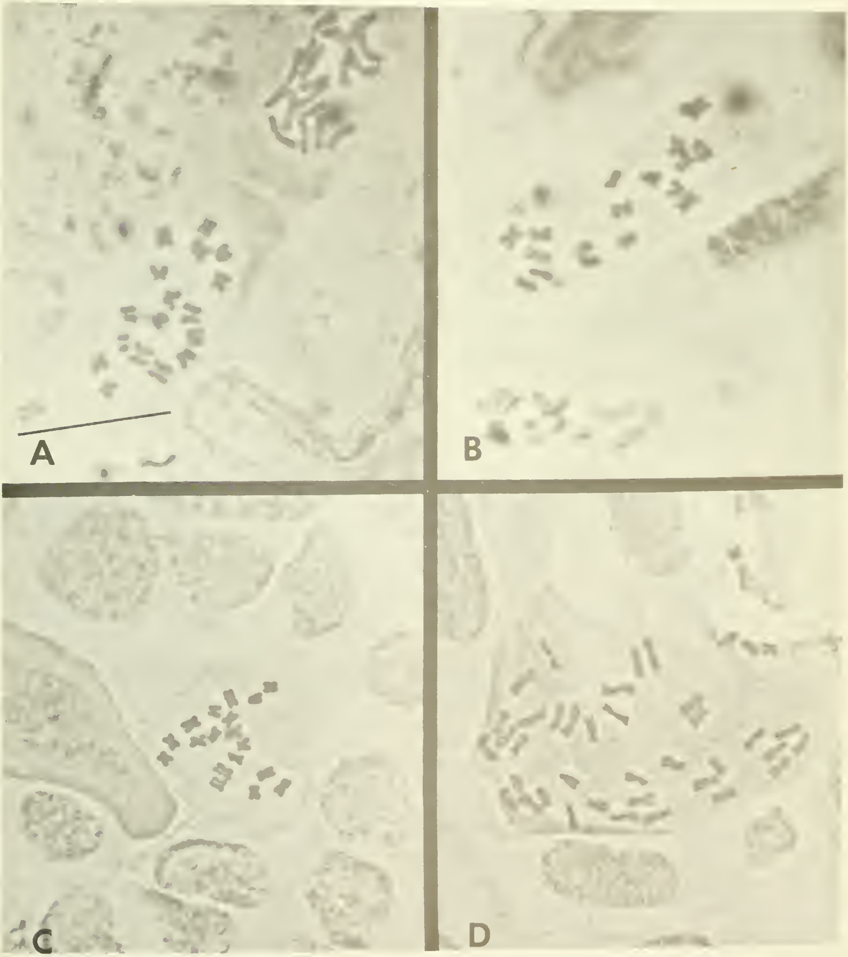

Fig. 1. *Artemisia* spp.: Photomicrographs of colchicine arrested metaphase plates of root tips (1400 X). A. *filifolia*, culture U7, $2n = 18$. B, *frigida*, culture U9, $2n = 18$. C, *spinescens*, culture U3, $2n = 18$. D, *spinescens*, culture U4, $2n = 36$. The line in Fig. 1A defines the end of a cell.

(McArthur and Plummer 1978). Each chromosome complement was assigned 100 arbitrary length units so that the actual measurement per chromosome was proportionalized. For diploid accessions, large chromosomes (L) were defined as those >12.6 units, medium (M) as 9.6–12.6, and small (S) <9.6. For the tetraploid accession, these values were halved. The centromere position was recorded as the proportional length of the short chromosome arm with respect to the length of the long arm. Metacentric chromosomes (M) were defined as those with a ratio >0.75, submetacentric (SM) as 0.50–0.75, and subteliocentric (ST) <0.50. Thus nine classes of chromosomes were possible: LST = large subteliocentric, LSM = large submetacentric, LM = large metacentric, MST = medium subteliocentric, MSM = medium submetacentric, MM = medium metacentric, SST = small subteliocentric, SSM = small submetacentric, SM = small metacentric. For preparation of the karyotypes of Table 3, chromosomes were grouped into the nine classes and paired by relative length and centromere position within each class. Interclass pairing was occasionally required so that all chromosomes could be paired. In such cases, length was given priority over centromere position. To confirm fit of pairing choices, each chromosome pair was visually inspected on the photomicrographs. The five samples for each accession were then averaged (x̄) for each chromosome pair and a standard error of the mean (se) computed.

A means of measuring karyotype asymmetry (Wiens and Richter 1966), F percent is obtained for a karyotype by averaging the proportional length of each short chromosome arm in respect to its long arm. In our case, F percent was obtained by halving the centromere position values of Table 3. As F percent decreases from a maximum of 50, a more asymmetric karyotype is indicated. Metaphase plates were available for *A. carruthii* (Keck 1946) and *A. frigida* (Knaben 1968). We compared our F percent results

Table 3. Karyotypic data for *Artemisia* species.

| Taxon | Accession | Chromosome characteristics[1] | 1 | 2 | 3 |
|---|---|---|---|---|---|
| *A. carruthii* | U4 | L | 12.75 ± .07 | 13.63 ± .24 | 12.18 ± .10 |
| | | C | .75 ± .05 | .90 ± .02 | .93 ± .03 |
| | | CC | LSM | LM | MM |
| *A. filifolia* | U7 | L | 14.12 ± .28 | 13.75 ± .33 | 12.63 ± .14 |
| | | C | .71 ± .02 | .92 ± .03 | .92 ± .03 |
| | | CC | LSM | LM | LM |
| *A. frigida* | U9 | L | 13.65 ± .33 | 10.59 ± .19 | 12.34 ± .22 |
| | | C | .92 ± .05 | .57 ± .07 | .96 ± .01 |
| | | CC | LM | MSM | MM |
| *A. spinescens* | U3 | L | 13.40 ± .16 | 12.11 ± .06 | 11.15 ± .20 |
| | | C | .78 ± .06 | .71 ± .05 | .64 ± .03 |
| | | CC | LM | MSM | MSM |
| *A. spinescens* | U4 | L | 6.71 ± .11 | 6.30 ± .04 | 6.91 ± .11 |
| | | C | .81 ± .02 | .82 ± .01 | .63 ± .02 |
| | | CC | LM | LM | LSM |
| | | | 10 | 11 | 12 |
| *A. spinescens* | U4 | L | 5.74 ± .03 | 5.62 ± .04 | 5.46 ± .06 |
| | | C | .89 ± .03 | .85 ± .03 | .84 ± .03 |
| | | CC | MM | MM | MM |

[1] Relative chromosome length (L), centromere position (C), and chromosome class (CC)

with values obtained from these previously published metaphase plates.

In order to compare the diploid ($2n = 18$) and tetraploid ($2n = 36$) chromosome complements of *A. spinescens*, we used a paired t-test (Woolf 1968). The assumption was that the relative lengths of the doubled pairs (1 with 2, 3 with 4, . . .17 with 18 of Table 3) would be significantly different ($P < 0.05$) from the diploid pairs (1,2,...9) if the diploid chromosome complement had not doubled to form the tetraploids. We point out that because size was the first pairing criterion, the possible doubled pairs' relative length of tetraploids are systematically biased (e.g.,1>2, 3>4, ...17>18). For centromere position, the average of tetraploid pairs was compared to the diploids (1 and 2 with 1, 3 and 4 with 2, ...17 and 18 with 9).

## Results and Discussion

The four diploid accessions have different, but not radically different, karyotypic patterns (Table 3, Fig. 1). Persson (1974:168) reported that the whole genus *Artemisia* has a relatively similar karyotype. We believe this tendency for a relatively similar karyotype is present in the genus, but some *Artemisia* taxa have quite different karyotypes (Filatova 1971, 1974a, 1974b), as well as probable aneuploid chromosome number reductions (Wiens and Richter 1966).

***Artemisia carruthii.***— The accession of *A. carruthii* that we examined has chromosome pairs as follows: 1 LSM, 1 LM, 5 MM, 1 SSM, and 1 SM (Table 3). *Artemisia carruthii* is a member of the *A. ludoviciana* Nutt. species complex of the subgenus Artemisia. It occurs in inland western North America and is known only as a diploid ($2n = 18$). Keck's (1946) metaphase plate has an F percent of 37 as compared to our 44. Despite the apparent difference, the chromosomes are probably similar. Estes's (1969) evidence (hybridization along with meiotic chromosome pairing) supported autopolyploidy in the *A. ludoviciana* complex.

***Artemisia frigida.***— Like *A. carruthii*, *A. frigida* is also a member of the subgenus Artemisia. *Artemisia frigida*, however, forms its

| Chromosome pair | | | | | | |
|---|---|---|---|---|---|---|
| 4 | 5 | 6 | 7 | 8 | 9 | F % |
| 11.45 ± .15<br>.90 ± .03<br>MM | 10.96 ± .14<br>.99 ± .01<br>MM | 10.65 ± .15<br>1.00 ± .00<br>MM | 10.43 ± .20<br>.79 ± .05<br>MM | 9.53 ± .29<br>.67 ± .06<br>SSM | 8.39 ± .16<br>.96 ± .02<br>SM | 44 |
| 9.99 ± .31<br>.50 ± .04<br>MSM | 11.89 ± .28<br>.90 ± .03<br>MM | 10.95 ± .32<br>.84 ± .04<br>MM | 10.10 ± .20<br>.97 ± .01<br>MM | 8.50 ± .38<br>.38 ± .02<br>SST | 9.05 ± .30<br>.86 ± .03<br>SM | 39 |
| 11.82 ± .16<br>.82 ± .04<br>MM | 11.32 ± .21<br>.98 ± .01<br>MM | 10.78 ± .18<br>.91 ± .08<br>MM | 10.53 ± .17<br>.96 ± .02<br>MM | 9.58 ± .13<br>.49 ± .02<br>SST | 9.36 ± .16<br>.85 ± .04<br>SM | 41 |
| 10.62 ± .21<br>.73 ± .08<br>MSM | 11.92 ± .19<br>.91 ± .05<br>MM | 11.34 ± .19<br>.87 ± .03<br>MM | 10.40 ± .13<br>.94 ± .05<br>MM | 9.78 ± .20<br>.85 ± .09<br>MM | 9.31 ± .14<br>.62 ± .07<br>SSM | 39 |
| 6.36 ± .08<br>.62 ± .02<br>LSM | 5.86 ± .12<br>.50 ± .05<br>MSM | 5.58 ± .13<br>.50 ± .05<br>MSM | 5.41 ± .09<br>.60 ± .04<br>MSM | 4.95 ± .06<br>.53 ± .03<br>MSM | 6.03 ± .04<br>.91 ± .01<br>MM | – |

| Chromosome pair | | | | | | |
|---|---|---|---|---|---|---|
| 13 | 14 | 15 | 16 | 17 | 18 | |
| 5.27 ± .10<br>.87 ± .03<br>MM | 5.22 ± .10<br>.87 ± .03<br>MM | 4.78 ± .06<br>.85 ± .05<br>SM | 4.60 ± .03<br>.87 ± .02<br>SM | 4.62 ± .10<br>.54 ± .06<br>SSM | 4.58 ± .11<br>.41 ± .02<br>SST | 36 |

own species complex. It ranges from Mexico through Alaska to Siberia (McArthur et al. 1979). *Artemisia frigida* is known only as a diploid ($2n = 18$) (Löve and Löve 1964, Knaben 1968, Kovanda 1972, Mulligan and Cody 1972, Hartman 1977, McArthur and Pope 1977). Its karyotype consists of 1 pair LM, 1 pair MSM, 5 pair MM, 1 pair SST, and a pair of SM chromosomes with an F percent of 41 (Table 3, Fig. 1A). Knaben's (1968) cell had an F percent of 43.

***Artemisia filifolia.***— This species is assigned to the subgenus Dracunculus, but has no close relatives (Hall and Clements 1923). Beetle (1979) recently suggested a possible affinity between *A. filifolia* and the Tridentatae. Our analyses show it to have pairs of chromosomes as follows: 1 LSM, 2 LM, 1 MSM, 3 MM, 1 SST, 1 SM with an F percent of 39 (Table 3, Fig. 1B). This karyotype is quite similar to the Tridentatae—differing by two chromosome pairs. The mean Tridentatae F percent is 38 (calculated from McArthur and Plummer 1978). When compared to the Tridentatae karyotype, *A. filifolia* has an extra LM pair in place of an MSM (McArthur and Plummer 1978). Kelsey and Shafizadeh (1979) point out that the sesquiterpene lactone colartin is shared by *A. filifolia* and the Tridentatae. Our chromatographic data (Hanks et al. 1973 and unpublished data stored at the Shrub Sciences Laboratory) of phenolic compounds also show some similarities between the two taxa. Before any close relationship can be inferred, however, more definitive chemotaxonomic and systematic study is required. The taxa differ widely in floral characteristics and wood anatomy (Moss 1940, McArthur 1979) and apparently do not hybridize despite areas of sympatric distribution.

***Artemisia spinescens.***— This species is also currently assigned to the subgenus Dracunculus (McArthur 1979). It differs from other species of *Artemisia* because it is both spring flowering and deciduous. Only four populations have had chromosome numbers determined (Powell et al. 1974, McArthur and Pope 1977). Of these, three were diploid ($2n = 18$) and one was tetraploid ($2n = 36$). In the present study, the diploid karyotype has 1 LM, 3 MSM, 4 MM, and 1 SSM chromosome pairs with an F percent of 39, whereas the tetraploid has a karyotype of 2 LSM, 2 LM, 4 MSM, 6 MM, 1 SST, 1 SSM, and 2 SM chromosome pairs with an F percent of 36. The tetraploid karyotype appears to be an approximate doubling of the diploid one. Our paired t-tests for relative length and centromere position showed tetraploid chromosomes to be about what would be expected in doubling the diploid chromosomes. The approximate doubling was especially true for relative length ($P < 0.50$). The centromere positions were not significantly different from doubling ($0.10 > P > 0.05$), but did not indicate an exact doubling. Another measure of centromere position, F percent, was about the same for the diploid and tetraploid accessions (Table 3).

Of particular interest were two pairs of LSM and SM and the single pairs of SST and SSM in the tetraploid. The LSM and SM could have been derived from the largest MSM and the smallest MM pairs (Pairs 3 and 8: Table 3) of the diploids by translocation. The SST and SSM pairs of the tetraploid could, with repatterning (e.g., pericentric inversions), have been derived from the diploid SSM pair 9. Persson (1974) illustrated the analogous nonsimilar $4x$ and $6x$ polyploid grouping that occurs in the *A. maritima* L. complex.

It is hard for us to visualize the tetraploid *A. spinescens* as anything other than autotetraploid. *Artemisia spinescens* has no close relatives. Although the diploid genome may have differentiated in various populations so that the tetraploid(s) may have arisen from hybrids between slightly different parents, the hypothetical differentiated diploids must surely have had a common source in the recent past. Further support for the autotetraploid nature of tetraploid *A. spinescens* is the apparent tendency for autopolyploidy in the genus *Artemisia*. Table 1 certainly suggests such a tendency. Furthermore both the *A. ludoviciana* (Estes 1969) and the *A. tridentata* (Ward 1953, McArthur and Plummer 1978) complexes are riddled with autopolyploidy.

## CONCLUSIONS

The four species examined in this report mirror much of the genus *Artemisia*'s chromosomal picture. Their karyotypes are, in general, quite similar although there are distinctive differences. The four species are all $x=9$, as is most of *Artemisia*. *Artemisia spinescens* shows apparent autopolyploidy, a phenomenon quite common in *Artemisia*. *Artemisia filifolia* has a karyotype quite similar to that found in the *A. tridentata* complex, but morphological and anatomical differences do not support a close relationship between these taxa.

## Acknowledgments

This study was aided by federal funds for wildlife habitat restoration through Pittman-Robertson W-82-R Project (Cooperators: Intermountain Forest and Range Experiment Station, USDA Forest Service, Ogden, Utah; and Utah State Division of Wildlife Resources, Salt Lake City, Utah). The Snow Field Station is cooperatively maintained by the above agencies, Utah State University, and Snow College.

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# VARIATION IN LEAF ANATOMY AND $CO_2$ ASSIMILATION IN *SITANION HYSTRIX* ECOTYPES

Warren P. Clary[2]

Abstract.— Collections of *Sitanion hystrix* known to differ in phenological development, height, dry matter production, and total water use were examined for possible differences in leaf anatomy and in $CO_2$ assimilation rates. Collections originating in warm, dry habitats produced the narrowest leaves with the fewest veins. Other anatomical characteristics examined were either not different among collections or the differences did not appear to be related to the original habitats. The $CO_2$ assimilation rates were similar on per-unit weight basis; therefore total assimilation varied as a function of plant size.

Ecotypic variation within plant species has been studied by a number of investigators to better understand how plants adapt to their environment. The ecotype concept, or the genotypic response of a species to environmental factors, had its roots in the 19th-century work of Jordan (Quinn and Ward 1969). Some of the most notable advancements of knowledge were made by Turesson in the 1920s; by Clausen, Keck, and Hiesey in the 1940s; and by McMillan in the 1950s. Ecotypic responses to climate are often through variation in phenology and dry matter production, whereas responses to grazing are often variation in growth forms and phenology. Responses to edaphic variation may be physiological rather than morphological or phenological.

Within grass species, differences occur in numbers of vascular bundles, in stomate density (Dobrenz et al. 1969a, 1969b), and in numbers of mesophyll cells (Wilson and Cooper 1969). Epidermal variations have been noted by Benson and Borrill (1969) and Gray et al. (1969). Photosynthetic and respiration rates have also been shown to vary within species (Klikoff 1968, Wilson and Cooper 1969). For grasses, however, it appears to the author that most within-species variation in internal structure and photosynthesis has been demonstrated among genotypes developed in plant-breeding programs, rather than among naturally occurring races.

The differentiation in response to climatic variation among *Sitanion hystrix* ecological races occurs in phenological development, height, dry matter production, and respiratory rate, but apparently not in water use efficiency (Klikoff 1968; Clary 1975). The purpose of this study of *Sitanion hystrix* leaf anatomy and $CO_2$ assimilation rates was to determine whether differences in these characteristics appeared to be ecotypic responses to climate of the collection sites.

## Methods and Materials

Clonal plant materials were collected in seven states to obtain samples from a wide variety of habitats and to provide ample opportunity for ecotypic differences to occur among the populations studied. Collections were made in South Dakota, Nebraska, Colorado, New Mexico, Arizona, Utah, and Nevada (Fig. 1). Collection sites varied as much as 13°33′ in longitude, 12°14′ in latitude, 1600 m in elevation, and 429 mm in annual precipitation (Table 1). These sites represent Merriam's ecological life zones of Upper Sonoran to Hudsonian (Lowe 1964).

The plants were divided into ramets and studied in a transplant garden and a growth chamber. General procedures followed, as well as the study conditions, can be found in Clary (1975).

Leaf Anatomy.— Leaf materials were gathered in the transplant garden during the first week of July for two years. Three leaves,

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[1] This article was written and prepared by U.S. government employees on official time and is therefore in the public domain

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one from the center of each of three randomly selected plants, were obtained from individual collections. These were killed and fixed in Craf III solution. The leaf samples were sectioned and stained with a safranin-fast green schedule.

The leaf cross sections were examined microscopically. An ocular micrometer was used to measure three samples per leaf for:

1. Thickness of outer abaxial epidermal wall plus cuticle;
2. Total thickness of abaxial epidermal cells (Fig. 2);
3. Cross-sectional area (height times width) of substomatal cavity;
4. Cross-sectional area (height times width) of bulliform cells; and
5. Width of leaf cross section.

The numbers of leaf veins were recorded in the following categories: (A) veins with a flattened top and a complete column of sclerenchyma fibers from upper to lower epidermis; (B) veins with a rounded top and an incomplete column of supporting tissue; and (C) veins with less than three-quarters the height of A and B category veins with an incomplete column of supporting tissue (Fig. 2). Thirty-five millimeter transparency photographs were taken of the leaf cross sections. These were projected onto a dot grid and the proportion of structural tissue (vascular bundles and sclerenchyma fibers) was determined.

Silicone rubber impressions (Zelitch 1961)

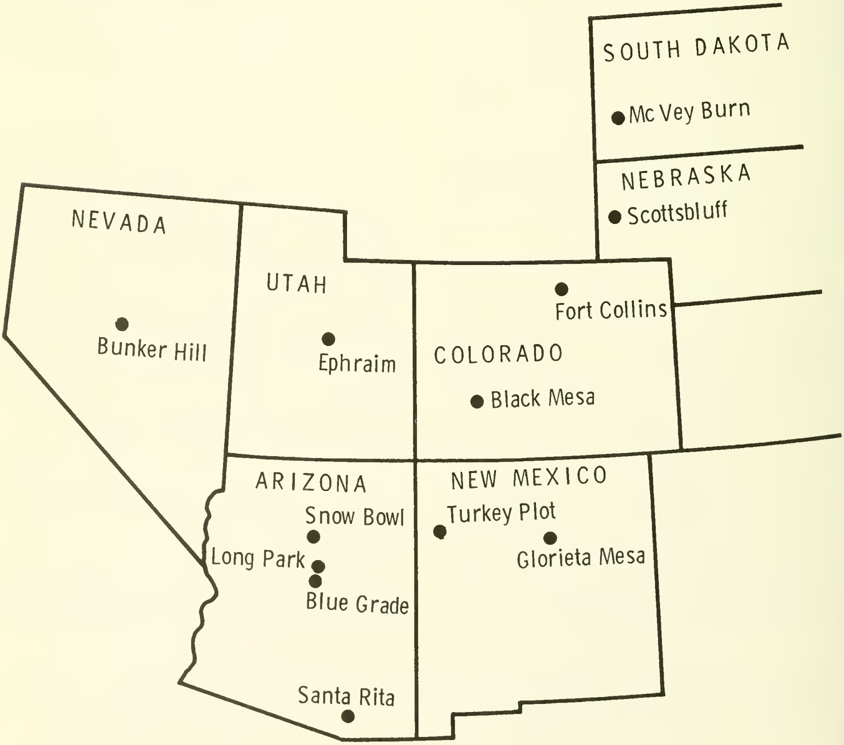
SOUTH DAKOTA
Mc Vey Burn
NEBRASKA
Scottsbluff
NEVADA
Bunker Hill
UTAH
Ephraim
Fort Collins
COLORADO
Black Mesa
ARIZONA
Snow Bowl
Long Park
Blue Grade
Santa Rita
NEW MEXICO
Turkey Plot
Glorieta Mesa

Fig. 1. Geographic distribution of the *Sitanion hystrix* collection sites.

were made of the abaxial leaf surface of three plants in each collection in the transplant garden. The adaxial surface was not used because deep venation obscured the stomata. A transparent positive was obtained by painting the rubber impressions with a thin film of cellulose acetate. Stomate density was determined by counting the number per microscope field. An ocular micrometer was utilized to determine the average length and width of the stomatal apparatus (stoma, guard cells, and subsidiary cells).

$CO_2$ ASSIMILATION.— Fifty-five potted ramets were used in a study of relative rates of $CO_2$ assimilation. A movable plexiglass assimilation chamber was constructed that could accommodate 10 plants at a time. The chamber was set inside a plant growth room so uniform conditions could be provided. Temperatures inside the assimilation chamber were never lower than 21 C nor higher than 27 C. Each replication was exposed for two hours to 50 $\mu$C of $C^{14}O_2$.

Four 2.54-cm leaf sections were immediately taken from each ramet. Alcohol extractions were made from two of the sections and beta particle emissions were counted with a GM tube and scaler. The remaining two sections were oven dried and weighed. Beta counts per unit weight of leaf were then calculated. The counts were considered an expression of $CO_2$ assimilation activity.

A second study of relative rates of $CO_2$ assimilation used *Sitanion hystrix* seedlings because previous observations indicated that plants grown from seed may have more uniform vigor than transplants. Seed was used from four sources: Blue Grade (Arizona), Snow Bowl (Arizona), Long Park (Arizona), and McVey Burn (South Dakota) (Fig. 1). Seventy-two 1.9-liter cartons, 18 per source, were filled with a commercial potting mix and planted with eight seeds. Regular watering maintained a moist substrate. After two weeks, the plants were thinned to four per carton. Assimilation rates were measured at eight weeks.

The procedure for extraction of $C^{14}$ from the seedlings was similar to that used for the ramets, except that the entire aerial portions of two plants from each carton were extracted and the aerial portions of the other two plants were oven dried and weighed.

TABLE 1.— Description of *Sitanion hystrix* collection sites.

| Collection site | Location | Elevation (m) | Precipitation (mm) | Climatic index[1] | Merriam life zone |
|---|---|---|---|---|---|
| Snow Bowl (north central Ariz.) | 111°42′W, 35°20′N | 2,980 | 739 | 0.93 | Hudsonian |
| Black Mesa (southwest Colo.) | 107°29′W, 38°30′N | 2,840 | 732 | 1.00 | Hudsonian |
| Bunker Hill (central Nev.) | 117°07′W, 39°18′N | 2,620 | – | – | Upper Sonoran |
| Turkey Plot (northwest N.M.) | 108°33′W, 35°25′N | 2,380 | 452 | .49 | Transition |
| Long Park (central Ariz.) | 111°29′W, 34°53′N | 2,260 | 574 | .59 | Transition |
| Glorieta Mesa (north central N.M.) | 105°41′W, 35°22′N | 2,200 | 406 | .43 | Upper Sonoran |
| Ephraim (central Utah) | 111°36′W, 39°18′N | 1,680 | 310 | .31 | Upper Sonoran |
| McVey Burn (western S.D.) | 103°34′W, 44°00′N | 1,520 | 516 | .62 | Transition |
| Fort Collins (northern Colo.) | 104°54′W, 40°36′N | 1,520 | 353 | .37 | Upper Sonoran |
| Blue Grade (central Ariz.) | 111°43′W, 34°43′N | 1,440 | 396 | .30 | Upper Sonoran |
| Scottsbluff (western Neb.) | 103°40′W, 42°00′N | 1,380 | 356 | .38 | Upper Sonoran |
| Santa Rita (southern Ariz.) | 110°51′W, 31°46′N | 1,380 | 498 | .30 | Upper Sonoran |

[1] Joint variable developed from relative growing season length and annual precipitation, and expressed as a proportion of the maximum value

STATISTICAL ANALYSES.— Analyses of variance were computed for leaf anatomy and assimilation data. A modified Tukey comparison (Snedecor 1956) was used where appropriate to isolate significant differences among means.

A climatic index was developed for the collection sites by multiplying an expression of growing season length times annual precipitation, and expressing the result as a proportion of the maximum value. This positioned each collection site on a scale of conditions from warm-dry to cool-wet. The numerical expression of growing season length was calculated by using the transplant garden as base 100. A value of one was added for each day later or subtracted for each day earlier than the transplant garden spring growth would normally be initiated at the collection sites (Hopkins 1918). This procedure produced larger values for short growing seasons and smaller values for long growing seasons. Plant characteristics were studied in relation to the climatic index (Table 1).

## RESULTS

Leaf widths varied significantly among collections. The narrowest leaves occurred in those collections from warmer and drier sites. Collections of *Sitanion hystrix* from such sites were previously reported to have lesser plant heights (Clary 1975), although the rankings for leaf width and maximum plant height are not highly correlated (r = 0.59). The relationship of leaf width to characteristics of the original collection sites has not been consistent among other grass species (Quinn 1969, Quinn and Ward 1969).

The collections with the widest leaves generally had the most veins per leaf. The total number of veins and vein categories A and C differed significantly among collections. The total veins per leaf appeared to be quite responsive to conditions of the original collection sites (Fig. 3). Plants from warm, dry habitats had the fewest veins per leaf. The numbers of veins were closely related to the climatic index of the collection sites and followed a consistent pattern in relation to Merriam's life zones.

Collections with the highest number of category A veins (McVey Burn, South Dakota; Long Park, Arizona; Turkey Plot, New Mexico; and Glorieta Mesa, New Mexico) were last to develop phenologically. These veins contain a greater concentration of structural tissue than do B and C category veins; thus, these results may support those of

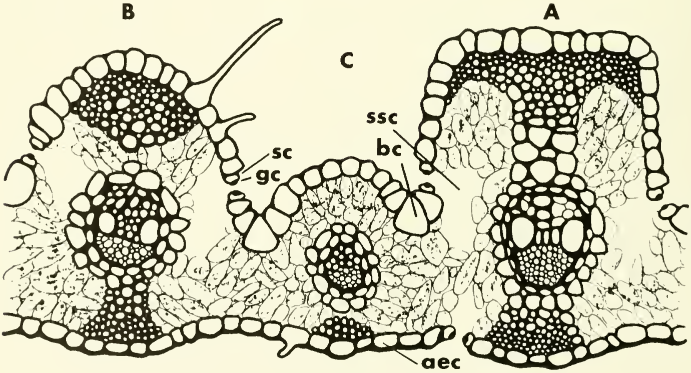

Fig. 2. Typical leaf cross section of *Sitanion hystrix*: A = Category A vein; B = Category B vein; C = Category C vein; aec = abaxial epidermal cell; bc = bulliform cell; gc = guard cell; sc = subsidiary cell; and ssc = substomatal cavity.

Christie and Mowat (1968). Those authors reported that the later the date of anthesis in *Dactylis glomerata,* the less digestible the plant to ruminant animals.

Among collections, there were no differences in vein density, thickness of outer abaxial epidermal wall, thickness of abaxial epidermal cells, and cross-sectional areas of substomatal cavities and bulliform cells, or leaf thickness. Significant statistical interactions occurred between collections and time for several anatomy variables (epidermal outer wall, leaf thickness, and B category veins), suggesting that the collections respond differently to differences in years. This may be to some extent the effect of timing growth to precipitation, although the differences in anatomy did not follow a predictable pattern.

Percent of supporting tissue, stomate density, and stomate width differed significantly among the collections, but the differences appeared to have no geographical or ecological relationships. Other investigators have reported significant and often distinctive variation in characteristics that had no apparent relation to environment (Quinn 1969, Quinn

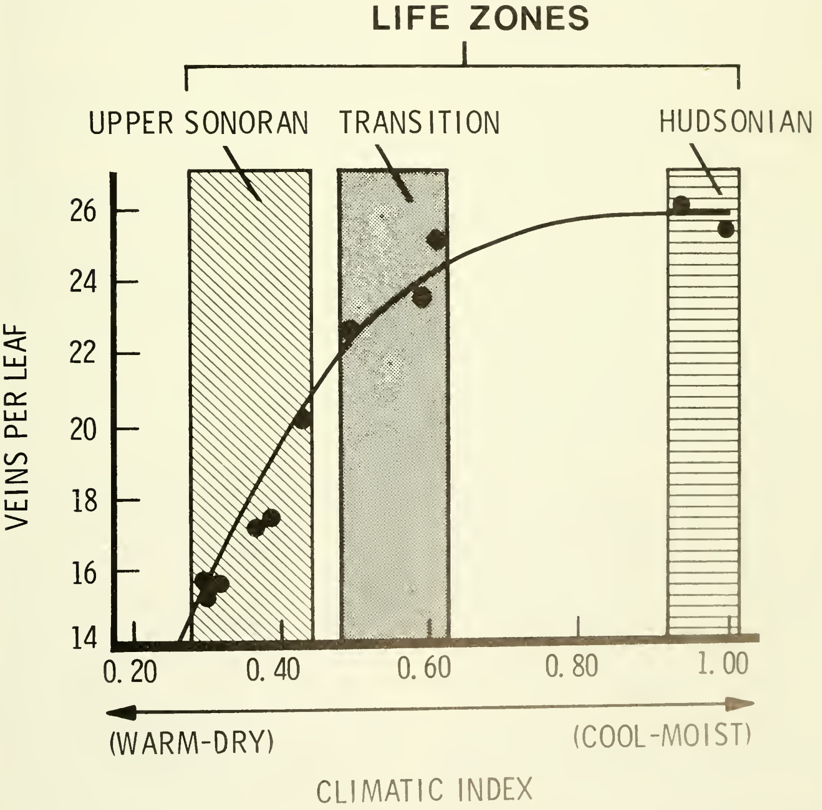

Fig. 3. Relationship of veins per leaf to two characterizations of the original collection sites—Merriam's life zones and a climatic index.

nd Ward 1969). This may be the result of lo al genetic drift, particularly for character tics that have little adaptive importance nd are not subject to strong selection pres ire.

Carbon dioxide assimilation rates were ieasured to obtain an index of photo ynthetic activity. Among collections, no dif erences were found in assimilation rates per nit weight of leaf in ramets or seedlings. As milation of $C^{14}$ was very closely related to ɔtal weight of seedlings ($r = 0.99$).

Assimilation rates were tested under only ne set of conditions. Respiration rates have een shown to differ among collections at ɔme temperatures, but not at others (Klikoff 968). The possibility thus exists that assimi tion rates would have varied among collec ons under different temperature regimens.

## Discussion

Considerable disagreement exists on the alue of variations in leaf structure to $CO_2$ ssimilation rates and efficiency of water use Ashton 1948, Maximov 1931, Shields 1950, nd Milthorpe 1961). The "xeromorphic" leaf ɔrm has often been considered important in nis regard. This form generally has a low ırface to volume ratio, decreased cell size, nicker cell walls, more compact network of eins, higher stomatal frequency, and thick ning of the cuticle. The characteristics mea ired in this study that most typify the xero norphic leaf form varied little among ɔllections.

In apparent harmony with this lack of eromorphic trends in arid habitat collections as the similarity among collections of assim ation rates or of water requirements (Clary 975). The total $CO_2$ assimilated and $H_2O$ anspired in a given period did not appear ) be a function of specific anatomical or hysiological adaptations, but largely a func on of plant size, which varied among collec ons.

A major form of adaptation by *Sitanion ystrix* populations has been to match their ming of growth to the most favorable peri d of the year, thus reducing the likelihood f severe moisture stress (Clary 1975). There ɔre, although the collections were from sites ith widely differing climatic conditions, there may have been little selection pressure on most populations to differentiate a more xeromorphic leaf anatomy.

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# INDEX TO VOLUME 39

The genera and species described as new to science in this volume appear in bold type in this index.

Allred, Dorald M., and Arthur C. Cole, article by, p. 97.
Allred, Dorald M., and Vasco M. Tanner, article by, p. 89.
Annual energy budgets for three common rodent species in the northern Great Basin, p. 143.
Anomiopsyllinae (Siphonaptera: Hystrichopsyllidae), II. The genera *Callistopsyllus, Conorhinopsylla, Megarthroglossus,* and *Stenistomera*, p. 351.
Ants from northern Arizona and southern Utah, p. 97.
Armstrong, David M., article by, p. 199.
Baumann, Richard W., article by, p. 241.
Beetles from the environs of Lake Powell in southern Utah and northern Arizona, p. 89.
Bee visitation of *Phlox bryoides* (Polemoniaceae), p. 197.
Bloss, Deborah Ann, and Jack D. Brotherson, article by, p. 161.
Booth, Gary M., David A. Stewart, and Jerold L. Petty, article by, p. 129.
Boraginaceae of the southwestern United States, p. 293.
Brothers, Donald R., article by, p. 195.
Brotherson, Jack D., and Deborah Ann Bloss, article by, p. 161.
Brotherson, Jack D., and Karen J. Brotherson, article by, p. 177.
Brotherson, Jack D., Lorin E. Squires, Mark C. Whiting, and Samuel R. Rushforth, article by, p. 245.
Brotherson, Jack D., and Michael G. Skougard, article by, p. 44.
Brotherson, Jack D., Shobha A. Jatkar, and Samuel R. Rushforth, article by, p. 15.
Brotherson, J. D., and E. M. Christensen, article by, p. 263.
Brotherson, Karen J., and Jack D. Brotherson, article by, p. 177.
Chemical composition of some important plants of southeastern Utah summer ranges related to mule deer reproduction, p. 122.
Christensen, E. M., and J. D. Brotherson, article by, p. 263.
Clary, Warren P., article by, p. 427.
Climates of fescue grasslands of mountains in the western United States, p. 284.
*Cnemonyx* **furvescens**, p. 137.
*Cnemonyx* **protivorus**, p. 137.
*Cnemonyx* **squamifer**, p. 138.
*Cnemonyx* **vismiacolens**, p. 138.
Cole, Arthur C., and Dorald M. Allred, article by, p. 97.
Competition between harvester ants and rodents in the cold desert, p. 267.
Competitive displacement as a factor influencing phytoplankton distribution in Utah Lake, Utah, p. 245.
*Corthylus* **nanus**, p. 138.
Craig, T. H., and R. L. Gleason, article by, p. 274.
Decreases of juniper woodland in the Utah and Salt Lake valleys since settlement, p. 263.
*Dendrocranulus* **auctus**, p. 139.
*Dendrocranulus* **limbellus**, p. 139.
*Dendrocranulus* **limitaris**, p. 140.
*Dendrocranulus* **modus**, p. 140.
*Dendrocranulus* **pinguis**, p. 140.
Diatom floristics and succession in a peat bog near Lily Lake, Summit County, Utah, p. 15.
Distribution of sculpins in the Clearwater River basin, Idaho, p. 59.
Ecological and community relationships of *Eriogonum corymbosum* (Polygonaceae) in the Uinta Basin, Utah, p. 177.
Ecological distribution of rodents in Canyonlands National Park, Utah, p. 199.
Emergence data and artificial rearing media for an aspen bark beetle, *Trypophloeus populi* (Coleoptera: Scolytidae), p. 129.
Feldhamer, George A., article by, p. 207.
First record of *Patapius spinosus* in Idaho

and Nevada (Hemiptera: Leptopodidae), p. 195.
Flinders, Jerran T., and Jeffrey S. Green, article by, p. 88.
Flora of the Lee Creek valley, Alberta, p. 277.
Food habits of burrowing owls in southeastern Idaho, p. 274.
Gleason, R. L., and T. H. Craig, article by, p. 274.
Green, Jeffrey S., and Jerran T. Flinders, article by, p. 88.
Ground nesting and aggressive behavior of the Swainson's Hawk (*Buteo swainsoni*) p. 253.
Harper, Kimball T., and John D. Shane, article by, p. 219.
Harper, K. T., and Jordan C. Pederson, article by, p. 122.
Heckmann, Richard A., Roger W. Mickelsen, and Rex C. Infanger, article by, p. 231.
Higgins, Larry C., article by, p. 293.
Homing by a pygmy rabbit, p. 88.
*Hylocurus* **clarki,** p. 141.
*Hylocurus* **longipennis,** p. 141.
Infanger, Rex C., Roger W. Mickelsen, and Richard A. Heckmann, article by, p. 231.
Influence of precipitation and temperature on ring, annual branch increment, and needle growth of White Fir and Douglas-fir in central Utah, p. 219.
Jatkar, Shobha A., Samuel R. Rushforth, and Jack D. Brotherson, article by, p. 15.
Jones, Stephen G., article by, p. 155.
Jorgensen, Clive D., and Vichitra Mongkolprasith, article by, p. 63.
Jorgensen, Clive D., Dan S. Landeen, and H. Duane Smith, article by, p. 267.
Karyotypes of four *Artemisia* species: *A. carruthii, A. filifolia, A. frigida*, and *A. spinescens*, p. 419.
Landeen, Dan S., Clive D. Jorgensen, and H. Duane Smith, article by, p. 267.
McArthur, E. Durant, and C. Lorenzo Pope, article by, p. 419.
McArthur, E. Durant, Charles F. Tiernan, and Bruce L. Welch, article by, p. 81.
Maughan, O. Eugene, and Gary E. Saul, article by, p. 59.
Mickelsen, Roger W., Richard A. Heckmann, and Rex C. Infanger, article by, p. 231.
Mongkolprasith, Vichitra, and Clive D. Jorgensen, article by, p. 63.
Mosher, James A., and Neil D. Woffinden, article by, p. 253.
Nash, Donald J., and David Wasserman, article by, p. 192.
Nearctic stonefly genera as indicators of ecological paramaters (Plecoptera: Insecta), p. 241.
New synonymy and new species of American bark beetles (Coleoptera: Scolytidae), Part VIII, p. 133.
Peabody, Frederick J., article by, p. 1.
Pederson, Jordan C., and K. T. Harper, article by, p. 122.
Petty, Jerold L., David A. Stewart, and Gary M. Booth, article by, p. 129.
Phytoseiid predators of mite pests in Utah apple orchards, p. 63.
*Phlox longifolia* Nutt. (Polemoniaceae) complex of North America, p. 1.
Pope, C. Lorenzo, and E. Durant McArthur, article by, p. 419.
Potential use of Great Salt Lake water for lobster culture, p. 231.
Preliminary survey of raptor species in the Manti Division, Manti-La Sal National Forest, p. 155.
Response of reptile populations to different land management practices on the Idaho National Engineering Laboratory Site, p. 255.
Review of tularemia in Utah and the Great Basin, p. 103.
Reynolds, Timothy D., article by, p. 255.
Rushforth, Samuel R., Lorin E. Squires, Mark C. Whiting, and Jack D. Brotherson, article by, p. 245.
Rushforth, Samuel R., Shobha A. Jatkar, and Jack D. Brotherson, article by, p. 15.
Saul, Gary E., and O. Eugene Maughan, article by, p. 59.
Schreiber, R. Kent, article by, 143.
*Scolytodes* **striatulus,** p. 136.
Shane, John D., and Kimball T. Harper, article by, p. 219.
Shaw, R. Keith, article by, p. 277.
Sheldon, Andrew L., article by, p. 289.
Skougard, Michael G., and Jack D. Brotherson, article by, p. 44.
Smith, H. Duane, Dan S. Landeen, and Clive D. Jorgensen, article by, p. 267.
Squires, Lorin E., Mark C. Whiting, Jack D. Brotherson, and Samuel R. Rushforth, article by, p. 245.

Stark, Harold E., article by, p. 103.
Stark, Harold E., Vernon J. Tipton, and John A. Wildie, article by, p. 351.
Stewart, David A., Gary M. Booth, and Jerold L. Petty, article by, p. 129.
Stonefly (Plecoptera) records from the basin ranges of Nevada and Utah, p. 289.
Studies in Nearctic desert sand dune Orthoptera, Part XVI: A new black *Stenopelmatus* from the Mescalero Sands, p. 226.
Subspecies specificity of gall forms on *Chrysothamnus nauseosus*, p. 81.
Tanner, Vasco M., and Dorald M. Allred, article by, p. 89.
Tepedino, V. J., article by, p. 197.
Tiernan, Charles F., E. Durant McArthur, and Bruce L. Welch, article by, p. 81.
Tinkham, Ernest R., article by, p. 226.
Tipton, Vernon J., Harold E. Stark, and John A. Wildie, article by, p. 351.
Variation in hemoglobin types in the Deer Mouse (*Peromyscus maniculatus*) along an altitudinal gradient, p. 192.
Variation in leaf anatomy and $CO_2$ assimilation in *Sitanion hystrix* ecotypes, p. 427.
Vegetational response to three environmental gradients in the salt playa near Goshen, Utah County, Utah, p. 44.
Vegetation response to a moisture gradient on an ephemeral stream in central Arizona, p. 161.
Vegetative and edaphic factors affecting abundance and distribution of small mammals in southeast Oregon, p. 207.
Wasserman, David, and Donald J. Nash, article by, p. 192.
Weaver, T., article by, p. 284.
Welch, Bruce L., E. Durant McArthur, and Charles F. Tiernan, article by, p. 81.
Whiting, Mark C., Lorin E. Squires, Jack D. Brotherson, and Samuel R. Rushforth, article by, p. 245.
Wildie, John A., Vernon J. Tipton, and Harold E. Stark, article by, p. 351.
Woffinden, Neil D., and James A. Mosher, article by, p. 253.
Wood, Stephen L., article by, p. 133.

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TABLE OF CONTENTS

Boraginaceae of the southwestern United States. Larry C. Higgins ............................ 293

Anomiopsyllinae (Siphonaptera: Hystrichopsyllidae), II. The genera *Callistopsyllus*, *Conorhinopsylla*, *Megarthroglossus*, and *Stenistomera*. Vernon J. Tipton, Harold E. Stark, and John A. Wildie ............................ 351

Karyotypes of four *Artemisia* species: *A. carruthii*, *A. filifolia*, *A. frigida*, and *A. spinescens*. E. Durant McArthur and C. Lorenzo Pope ............................ 419

Variation in leaf anatomy and $Co_2$ assimilation in *Sitanion hystrix* ecotypes. Warren P. Clary ............................ 427

Index to Volume 39 ............................ 433

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